ANATOMY OF THE MOUTH-PARTS

AND OF THE SUCKING APPARATUS

OF SOME DIPTERA.

DISSERTATION

FOR THE PURPOSE OF OBTAINING

THE PHILOSOPHICAL DOCTORATE

AT THE LEIPZIG UNIVERSITY,

BY

GEORGE DIMMOCK,
OF CAMBRIDGE, MASS., U. S. A.

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The few diptera whose mouth-parts have been the object of the anatomical studies, the results of which are noted in the following pages, were chosen, on the one hand, with especial reference to their presenting a series beginning with a species possessing simple, separate and fully developed mouth-parts, and ending with a species of which the complexity of the mouth-parts was due to coalescence and incomplete development of their different elements, and, on the other hand, with partial reference to forms whose mouth-parts were of sufficient length to render their study by sections, made with the microtome, of value in determining their relative lengths, their positions and their attachments. With the above-mentioned objects in view species of the genera *Culex*, *Bombylius*, *Eristalis*, and *Musca* were chosen. Upon the anatomy of the mouth-parts of *Culex* the following notes probably add most to what has been previously recorded. No study of the development of the mouth-parts has been made in preparing the following paper; the results are anatomical only.

The work necessary for the preparation of this paper was done by me, as student, in the Laboratory of the Zoological Institute in Leipzig, and I gladly take this opportunity of expressing my sincerest thanks to its director, my honored instructor, Professor Leuckart, for the advice and encouragement which he has given me in my studies.

HISTORICAL.

Until Fabricius, in 1775, first called attention to the importance of the mouth-parts in the classification of insects, little or no valuable progress had been made in the study of their comparative anatomy. Observations on the anatomy of the mouth-parts of single insects are to be found in the works of many writers, previous to the above-mentioned date, but they can be best regarded as forming only a part of the history of the anatomy of single insects, and, so far as they treat of insects which are further discussed in this paper, they will be mentioned later.

Fabricius writes, in the preface of his *Systema entomologiae*, [1] after discussing the confusion which existed in the classification of insects at his time, "Therefore I will try a new method, choosing characters, both of classes and of genera, from the mouth-parts. These parts truly offer sufficient and constant characters and far more natural genera." * In his *Philosophia entomologica* [2] (p. 37-52), where his ideas are further elaborated, one finds that Fabricius divided the mouth-parts of insects into palpi, clypeus (now the labrum), mandibulae, maxillae, galea, labium, lingua, rostrum, proboscis and haustellum. The proboscis and haustellum, the parts which concern us most here, are somewhat confused in Fabricius' classification. The proboscis, he writes (p. 38), is membranaceous and bilabiate; the haustellum is extended, chitinous, and without articulations; ** with the former is no mention of setae, with the latter, he adds, setae differing in number. He writes (p. 49), "The proboscis, so peculiar to the diptera, is not possessed by all of them," *** and, on the next page he gives *Bombylius* as without proboscis. Again he writes (p. 52), "The proboscis differs from the haustellum in that the proboscis is always bilabiate, the haustellum never," † and that, "The haustellum, being the characteristic of the class, is always present in the diptera; the proboscis is often entirely absent." †† Furthermore Fabricius writes (p. 39), "In the diptera are two palpi, a haustellum very often received in a proboscis, while mandibles, maxillae, clypeus and labium are absent." ††† From the above quotations it is clear that Fabricius meant by the proboscis what is now known to be, for the most part, labium; by haustellum, following the derivation of the word, he meant the true suction-tube, whether of one part, or made up of setae. The confusion which arises in the Fabrician use of proboscis and haustellum is mainly due to his failing to recognize, in his so-called "haustellum" of *Culex* and *Bombylius*, parts which correspond to his "proboscis" in *Musca*, *Syrphus* and other diptera.

[1] For full titles referred to by superior figures, see Literature at the end of this paper.

* "Novam ideo viam tentabo, characteres et classium et generum ex instrumentis cibariis desumens. Praebent sane sufficientes, praebent constantes et genera multo naturaliora."

** "Proboscis membranacea, bilabiata" . . . . . "Haustellum porrectum, corneum, inarticulatum."

*** "Proboscis tantum Antliatis propria, nec omnia illa ea gaudent."

† "Proboscis differt ab haustello, quod proboscis semper bilabiata, haustellum vero nunquam."

†† "Haustellum, classis continens characterem, semper in Antliatis adest, proboscis saepe omnino deest."

††† "Palpi duo, haustellum saepius proboscide receptum, absque mandibulis, maxillis, clypeo et labio in Antliatis."

Since Fabricius' time the terms proboscis and haustellum have been used somewhat indefinitely. Gerstfeldt sought to explain (p. 13 of his dissertation[3]) Fabricius' meaning, but seems to have failed in clearly comprehending the difference which the latter intended to establish between proboscis and haustellum. In the course of this paper proboscis will be used, in its generally accepted meaning at present, as a designation for such of the mouth-parts of diptera, taken together, as form their more or less flexible, shorter or longer, sucking apparatus.

According to J. V. Carus (Geschichte der Zoologie, p. 559) Fabricius also divided the insects into sucking and chewing species, a classification followed later by Clairville,[4] Lamarck, Gravenhorst, and many others.

Savigny,[5] in 1816, took the next important step in advancing our knowledge of the mouth-parts of insects, and showed that all the mouth-parts of insects were reducible to the same plan, that is to the plan which they present in chewing insects. Most of Savigny's work was done on lepidoptera, because the lepidoptera were supposed to have mouth-parts farthest removed in structure from those of chewing insects. Savigny says (p. 10-11), "I am convinced that, when one shall have better examined the mouth of the insects properly speaking, that is to say those with six feet and two antennae, one will find that, whatever form it may assume, it is always essentially composed of the same elements." ... "One discovers that the organ is the same; the use alone is modified or changed. See the constant plan of nature. Thus I think I can assert, from this time on, that the mouth of the diptera is formed of the same parts as that of the hymenoptera. But to prove this proposition it is necessary to commence by explaining the organization of the mouth of the hymenoptera." * Savigny says further (p. 13-14), "The mouth of the hymenoptera is, then, composed of four unpaired organs, without including the jaw or mentum; namely, the upper lip, the epipharynx, the hypopharynx and the under lip; and of two pairs of organs, the mandibles and the maxillae. The same organs are all found, either separately or simultaneously in the mouth of the diptera. The under lip exists almost always; it constitutes the proboscis, properly speaking. The maxillae exist likewise almost always; it is these organs which bear the palpi, so that the

* "Je suis convaincu que, lorsqu'on aura mieux examiné la bouche des insectes proprement dits, c'est-à-dire, à six pattes et à deux antennes, on trouvera que, quelque forme qu'elle affecte, elle est toujours essentiellement composée des mêmes éléments." .... "On sait que l'organe est le même: l'usage seul est modifié ou changé. Voilà le plan constant de la nature. Ainsi je crois pouvoir assurer dès à présent que la bouche des Diptères est formée des mêmes parties que celle des Hyménoptères. Mais pour démontrer cette proposition, il faudrait commencer par exposer l'organisation de la bouche des Hyménoptères."

diptera have two maxillary palpi and have no labial palpi. When the maxillae are apparently absent, as in the flies properly speaking, they coalesce with the under lip. The mandibles are found only in certain genera; they are, for example, very evident in the breeze-flies, where they have the form of two slender blades. The hypopharynx and epipharynx are the bristle, or the two intervening bristles. The upper lip is a bristle or broader scale which covers the others." *

Savigny did not stop with the reduction of the mouth-parts of all insects to a common plan, a result which seemed fairly to complete the work begun by Fabricius, but, in his second memoir, recognizing the resemblance between the mouth-parts of hexapods and those of the remaining arthropods (which he terms apiropods), and the graduated forms between the locomotory and manducatory appendages of some of these apiropods, he concludes (p. 43) that, "among these last apiropods [by which he means *Limulus*, *Apus*, etc.] the organs which serve for manducation do not essentially differ from those which, among the first apiropods [meaning *Iulus*, *Scolopendra*, and the like], and among the hexapods, serve for locomotion." ** Here was a direct homologizing of the mouth-parts of insects with locomotory organs, a theory which Savigny had publicly advanced as early as October 1814. *** The comparison of the paired appendages of spiders, scolopendra, and crustacea, which follows (p. 43-66 and 83-101) in his memoir, has little interest in connection with the study of diptera.

After Savigny had thus led the way, by his theories that all mouth-parts of insects were modifications of the same general plan, and that the paired mouth-parts were serial homologs of legs, little was left in the way of general theories

* "Voilà donc la bouche des Hyménoptères composée de quatre organes impaires, sans y comprendre la ganache ou le menton; savoir: la lèvre supérieure, l'épipharynx, l'hypopharynx et la lèvre inférieure, et de deux organes paires, les mandibules et les mâchoires. Les mêmes organes se retrouvent tous, soit séparément, soit simultanément, dans la bouche des Diptères. La lèvre inférieure existe presque toujours; elle constitue la trompe proprement dite. Les mâchoires existent de même presque toujours: ce sont elles qui portent les palpes, de sorte que les Diptères ont deux palpes maxillaires, et n'ont point de palpes labiaux. Quand les mâchoires semblent disparaître, comme dans les Mouches proprement dites, c'est qu'elles se confondent avec la lèvre inférieure. Les mandibules ne s'observent que dans quelques genres: elles sont, par exemple, très-visible dans les Taons, où elles ont la forme de deux lames très-déliées. L'hypopharynx et l'épipharynx sont la soie, ou les deux soies intermédiaires. La lèvre supérieure est une soie ou écaille plus large qui couvre les autres."

** Chez ces derniers Apiropodes, les organes qui servent à la manducation ne diffèrent pas essentiellement de ceux qui, chez les premiers Apiropodes et chez les Hexapodes, servent à la locomotion."

*** See foot-note of p. 43 of Savigny's second memoir.

which later investigators could advance, and we consequently find them confining their attention to minor anatomical points, or to discussions of how many and which of the mouth-parts are really homologs of legs, and to homologizing the coxal, femoral, tibial, or tarsal parts of insects' legs with portions of their mouth-parts. Savigny had already expressed his opinion (p. 41 of his second memoir), that, besides the paired organs, the under lip "can be considered as formed by the union of the two second maxillae." *

Erichson,[6] in 1840 (p. 4-7 of his *Entomographien*), discusses the mouth-parts of insects, devoting the greater part of his space to the consideration of the under lip, which he regarded as originating in the union of a pair of organs, in fact, speaking of it throughout his paper as the third pair of jaws. ** He says (p. 4-5) "The third mandibular pair forms, in insects proper, a constant part of the under lip, which is formed by the union of this pair with the mentum and with the tongue (ligula). This third pair has the mentum behind and beneath, and the ligula above and before it, but is always characterized by labial palpi which belong to it." *** He further adds (p. 7), "In the two other orders of insects with sucking mouth-parts, the diptera and hemiptera, the coalescence of the third pair extends still further upon the palpi, which form the tubes of the proboscis, and surround the remaining bristle-formed mouth-parts." † In the male of *Culex* I have found, as will be more fully described later, a somewhat analogous case of union of the tongue with the labium; that is, analogous, if one assumes the tongue, of Erichson, to be the hypopharynx, of Savigny, an assumption which may be incorrect, since Erichson fails to define clearly what he means by tongue, or ligula. It is furthermore very probable that, as Savigny stated, the labial palpi are absent in diptera, and I find nothing, in my own observations, or in those of others so far as I have compared them, to show that the proboscis of diptera is, in any way, the product of labial palpi. The homologies found in Erichson's paper are of doubtful value, at least so far as

* "Qu'on peut considérer comme formée par la réunion des deux secondes mâchoires."

** "Das dritte Kieferpaar."

*** "Das dritte Kieferpaar macht bei den eigentlichen Insecten beständig einen Theil der Unterlippe aus, welche durch die Vereinigung desselben mit dem Kinn (*mentum*) und der Zunge (*ligula*) gebildet wird. Dieses dritte Kieferpaar hat nun das Kinn hinter und unter, und die Zunge über und vor sich, wird indess immer durch die ihm angehörenden Lippentaster bemerkbar."

† "Bei den beiden andern Ordnungen der Insecten mit saugenden Mundtheilen, den Dipteren und den Hemipteren, erstreckt sich das Verwachsen des dritten Kieferpaares noch weiter auf die Taster, welche die Röhre des Rüssels bilden, und die übrigen borstenförmigen Mundtheile umschliessen."

they concern insects with sucking mouth-parts, because that, up to his time, and indeed up to the present time, no sufficiently careful work has been done on these parts to warrant such general conclusions as he pronounces.

The next important paper, in chronological order, upon the mouth-parts of insects was by Brullé,[7] in 1844. I have not seen this paper, but I am able to give a brief resumé of the author's views, from the reviews of his paper which appear in the dissertation by Gerstfeldt [3] (p. 5-9), in a paper by Menzbier [8] (p. 18-19), and in Erichson's *Bericht über die wissenschaftlichen Leistungen im Gebiete der Entomologie* (1844, p. 3-4). Savigny had regarded the labrum, epipharynx, and hypopharynx, as unpaired organs. Brullé sought to include these three organs in the system of paired appendages, which Savigny had established for the mandibles, maxillae and labium. Brullé considered the insect's head as made up of six segments, each with a pair of appendages, or with an unpaired appendage which owed its origin to the coalescence of a pair of appendages. The first segment consequently bore the labrum, the second the epipharynx, the third the hypopharynx, the fourth the mandibles, the fifth the maxillae, and the sixth the labium.

Blanchard,[9] in 1850, considered that the most important modifications of the mouth-parts of diptera were caused by coalescence of parts, and endeavored to support his views by the origin of the nerves which go to these parts. In the *Asilidae,* where only four setae are present, he regarded the mandibles as present, but grown together to form what is now termed the hypopharynx. In the *Muscidae,* and in other diptera with two setae, the mandibles were united to form the hypopharynx, and the maxillae coalesced with the labium. The above-expressed view that the so-called hypopharynx is composed of two mandibles grown together, a theory followed in Cuvier's *Regne Animal,* does not seem so improbable as it otherwise would in the light of Weismann's [10] statement (p. 190) that, in the *Muscidae* "The mandibular seta arises by coalescence of paired pieces, which surround, like the two halves of a sheath, a cylindrical chain of cells which tapers anteriorly. The cell-chain becomes the salivary duct, which in the imago comes from behind to the under surface of the seta, so as to unite with it and to open out a little behind its point with a fine opening." *

Gerstfeldt,[3] in 1853, (p. 13-47) discusses the mouth-parts of diptera. After

* "Die Kieferborste entsteht durch Verwachsung paariger Stücke, welche einen cylindrischen, nach vorn sich verjüngenden Zellenstrang umschliessen, wie die zwei Hälften eines Futterals. Der Strang wird zum Ausführungsgang der Speicheldrüsen, der in der Imago von hinten her an die untere Fläche der Borste tritt, um mit ihr zu verwachsen und etwas vor der Spitze mit feiner Oeffnung auszumünden."

preliminary remarks on the nature, size, direction, and general form of the proboscis, the author considers the parts and their nomenclature according to previous authors. His compilation of authorities is very complete. In a few words, the author's own views may be condensed as follows: The proboscis of the diptera consists of a sheath and its enclosed setae, or bristles. The sheath is made up, sometimes of the labium alone, sometimes of the labium as the chief portion, together with other mouth-parts; it can be regarded as consisting of three parts, the basis, the stem or stalk, and the end-lobes (labellae of Kirby). The setae or bristles enclosed in the sheath represent the remaining mouth-parts, and are either given as two, four, or six; or as one, three, or five; according as whether one includes the labrum with them or not. The labrum is more or less elongated, sometimes with a longitudinal furrow in the middle, supposed by Gerstfeldt to be an indication that this mouth-part was composed originally of lateral halves. The other setae, when they are all present, are the mandibles, maxillae and hypopharynx. Parts of the mandibles or maxillae sometimes unite with the labium to help form the sheath. The hypopharynx, or tongue, is absent in very few diptera. The epipharynx perhaps exists in a few cases, according to Gerstfeldt (p. 21), altho he says he has nowhere seen it. At the basis of the proboscis are regularly, if not invariably, two more or less developed palpi. Following the portions of Gerstfeldt's paper, of which the preceeding is an abstract, is a brief description of the mouth-parts, their mode of coalescence, and their presence or absence, in different families and genera of the diptera, beginning with diptera having two setae and ending with those having six.

Gerstfeldt's work was based, as is apparent from his introductory remarks (p. 4-5), on the view of Brullé that *all* the mouth-parts of insects were reducible to the modification of six pairs of appendages, themselves serial homologs of the thoracic ambulatory appendages. The theory seems to have been assumed at the outset of the author's work, and, therefore, to have had too much influence on the conclusions which Gerstfeldt drew from his otherwise, in general, accurate observations, for Gerstfeldt examined a large variety of material in the preparation of his paper, and examined it carefully, as far as the instruments at the disposal of anatomists of his time would allow. His failure, however, to recognize the epipharynx in diptera led him to make a curious mistake. He has described, as Menzbier [8] correctly observes (p. 65), the epipharynx of *Musca* freed from the labrum as the hypopharynx, and failed to discover the true hypopharynx. He regarded the longitudinal "suture" (probably in reality the channel) of the epipharynx (his hypopharynx), as an indication that the hypopharynx owes its origin to the coalescence of paired organs. Another mistake which Gerstfeldt

made in regard to the mandibles of *Culex* will receive notice later, in the description of those parts.

Passing over a number of works, which dealt with the anatomy of single species, or which had for their object the elucidation of the anatomy of special organs, the next important discussion of the mouth-parts of diptera is by Menzbier.

Menzbier,[8] in 1880, devotes the first twenty pages of his paper to a critical historical synopsis of the works in which the mouth-parts of diptera have been especially considered, and sixteen pages further to a critical historical summary of the literature which treats of the development of the chitin covering and appendages of insects, and to the results of the studies of Weismann, Kunckel d'Herculais, and others, upon the histoblasts, or imaginal disks. Succeeding the historical part of his paper, Menzbier details the results of his own investigations. After enumerating the regions of the head, according to his ideas of its structure, he explains (p. 53-66) the mouth-parts of *Haematopota*, *Syrphus*, *Empis*, *Musca* and *Sargus*, these genera representing a series, in which the first has all the typical mouth-parts of a chewing insect, and the last only the labrum, labium, and maxillary palpi. Menzbier seems to have been the first to recognize the usual intimate union of the labrum and epipharynx in diptera, where he finds them often separable by maceration in caustic potash. The following tabulation gives, at a glance, the more important points in Menzbier's paper, in regard to the mouth-parts of those diptera which he studied.

	Labrum and Epipharynx.	Hypopharynx	Mandibles.	Maxillae.	Labium.
Haematopota and *Chrysops.*	Separable in caustic potash.	lamelliform with channel on upper surface.	lamelliform	acicular. with palpi.	muscular.
Syrphus taeniatus.	do.	do.	do.	palpi only.	do.
Empis livida.	Not separable in caustic potash.	do.	absent.	united to form an unpaired needle, with palpi.	Bilobed at tip.
Musca species, *Sarcophaga carnaria* *Stomoxys calcitrans.*	Separable in caustic potash.	do.	do.	palpi only.	muscular.
Sargus nubeculosus.	Labrum present, epipharynx absent.	absent.	do.	do.	fleshy.

The fulcrum, which Gerstfeldt regarded as united maxillae, Menzbier considers to be chitinized processes of the oesophagus.

That the maxillae are grown together in *Empis livida,* is, perhaps, an error. My having no specimens of *Empis* prevented my proving this point. Gerstfeldt writes (p. 31-32), "Four setae — which always represent the maxillae, the upper lip and the hypopharynx, while the mandibles are united with the sheath of the proboscis — are found in the *Empidae* (in *Empis* the maxillae are also shorter than the hypopharynx, but this exceeds the upper lip; all four setae are pointed and horny)." *

After recording some of his observations on the development of the epipharynx and hypopharynx, Menzbier closes with a summary of his conclusions, which would he superfluous, if transcribed here.

With this short resumé of the advances made in the study of the general structure of the mouth-parts of insects, especially those of diptera, I will pass on to the recording of results of my own observations on single genera, prefixing to my own remarks, brief notices of the work done by others in the same direction.

ANATOMY OF THE MOUTH-PARTS OF *CULEX.*

From early times *Culex* has attracted the attention of mankind, but, until about two centuries ago, little or no progress was made in the knowledge of the inner structure of its mouth-parts.

Swammerdamm, [11] who studied *Culex* in 1668, distinguished the male and female, but evidently supposed that the structure of the proboscis of both sexes was the same. He correctly distinguishes the long maxillary palpi of the males from the short palpi of the females. He clearly recognized that there were six mouth-parts enclosed in a sheath, but erroneously supposed them to be protrusile from the end of the sheath, without flexion of the latter, and thus figured them. The largest of these enclosed mouth-parts (really the combined labrum and epipharynx) he supposed enclosed the other five, and he says (p. 147 of the German edition of 1752), "I regard it that these five setae serve, like as many sharp little awls to make the opening in the sweat-pores of the skin. When this is done they draw themselves back again into the inner sheath. This then

* "Vier Borsten — die immer den Maxillen, der Oberlippe und dem hypopharynx entsprechen, während die Mandiblen mit der Rüsselscheide verschmolzen sind — besitzen" . . . "die *Empiden* (bei *Empis* sind die Maxillen ebenfalls kürzer als der hypopharynx, dieser überragt aber die Oberlippe; alle vier Borsten sind zugespitzt und hornig)." . . .

enters (according to my idea) into the wound with its sharp cavity, and the mosquito sucks through it the blood, which ascends alongside and between the little setae into the belly of the mosquito." * The apical opening of this inner sheath he correctly thought to be turned toward the ventral side.

Leeuwenhoek next endeavored to settle the structure of the proboscis of *Culex*. All that I know of his work is from what Réaumur [12] (13 h mémoire, t. 4, p. 401-403) says of it. Leeuwenhoek found only four setae in the sheath of the proboscis, and doubted that the inner sheath, described by Swammerdamm, existed as a closed tube. Barth, [13] on the other hand, in 1737, according to Réaumur (l. c., p. 403), thought the inner sheath was a closed tube and not a channel.

Réaumur, [12] in 1738, published his description of the mouth-parts of *Culex*, and of their mode of biting; to the latter subject he gave much attention, and was the first to describe correctly how the sheath was disposed of during the use of the setae within, in the act of biting. He also calls attention to the poisonous effects of the bite, and, contrary to the views of Leeuwenhoek, who thought the inflammation following the bite of *Culex* was due to the peculiar nature of the wound itself, that is, that they were the natural consequences of a wound made by an instrument of a particular form, Réaumur regarded the subsequent inflammation of the place bitten by *Culex* to be due to a poisonous liquid which the insect injects into the wound, in order to cause the blood to flow faster. Réaumur found only five of the six setae which the proboscis contains. He favored the idea that the inner sheath, which Swammerdamm had described, was not cylindrical, but only a channel open on one side. Réaumur also arrived at the idea that the maxillary palpi of *Culex* could, in some cases, help to form the sheath which encloses the setae, but he does not clearly say that they always do so in the males.

Since Réaumur's time but little has been added to our knowledge of the mouth-parts of *Culex*, some writers following the statements of Swammerdamm, others those of Réaumur, or of Leeuwenhoek, in regard to the number of setae. Among others I will cite Sulzer [14] (1761), who says "four to five pointed tubules;" **

* "Ich halte davor, diese fünf Angelgen dienen dazu, als mit so viel spitzigen Pfriemgen die Oeffnung in den Schweisslöchern der Haut zu machen. Wenn dass gethan, so ziehen sie sich wiederum in die innere Scheide zurück. Diese dringt dann (nach meinem Begriff) mit ihrer spitzigen Höhle in die Wunde hinein, und die Mücke saugt durch sie das Blut in sich, das neben und zwischen den kleinen Angeln hin in den Bauch der Mücke hinaufsteigt."

** "4—5 spitzigen Röhrchen." (p. 169.)

Fabricius [1] (1775), who writes, "sheath exserted, univalvular, flexible, with five setae;" * Jördens [18] (1801) describes four setae; ** Gravenhorst [15] (1817), "The proboscis long, setiform, five-parted; *** Meigen [16] (1818) describes four setae and figures five; † Gerstfeldt [3] (1853), "The sheath is formed of the under lip alone, and contains six setae;" †† Packard [17] (1869), "These six bristle-like organs are folded together within the hollowed labium;" ††† Claus [19] (1876) writes, proboscis "extended with four setae." §

Roffredi's paper,[20] in 1769, upon the mouth-parts of *Culex*, I know only by title.

Without being unduly influenced by one or another of the authorities above mentioned, I will set forth the structure of the mouth-parts of *Culex*, both male and female, as I have found them in my own observations, in the following pages.

THE MOUTH-PARTS OF *CULEX*, FEMALE.

The mouth-parts which form the proboscis of the female *Culex*, as I have found them by study of *C. rufus*, *C. ciliatus* and *C. pipiens*, represent all the typical mouth-parts of different insects, and consist of a labrum (Pl. 1, fig. 1, *lr.*), an epipharynx (*e*), a hypopharynx (*h*), two mandibles (*m*) and two maxillae (*mx*), all sheathed, when in repose, in the labium (*l*), which receives them into a groove on its upper side. Each maxilla has a maxillary palpus (*m p*) which lies outside, and at the base of, the labium; the latter has no palpi, unless one regards, as Erichson did, the lobes at its tip to be palpi. Of these mouth-parts the labium and maxillary palpi are covered with hair and scales, the others are naked, light brown, setiform and transparent; they all originate at the anterior basal portion of the head, below the eyes and antennae (*a*), and are, with the exception of the maxillary palpi, of about equal lengths, that is, about three to four times the length of the head. The maxillary palpi, in the females of *Culex* proper, are about the length of the head. Those mouth-parts which are without scales, and

* "Vagina exserta, univalvis, flexilis, setis quinque." (p. 799.)

** P. 162, of Band I.

*** "Der Rüssel lang, borstenförmig, fünftheilig." (p. 44.)

† P. 2 and pl. 1 of Theil I.

†† "Die Scheide wird von der Unterlippe allein gebildet und enthält sechs Borsten," (p. 32.)

††† P. 369-370.

§ "Vorgestreckt mit 4 Stechborsten." (p. 682.)

these are the ones that penetrate the skin in biting, are not jointed; the labium of the female *Culex* is not jointed throughout its length, but the lobes, or labellae (Fig. 3 and 4, *lb*), are jointed to it, by a true joint, near its tip; the maxillary palpi are sometimes four-jointed, sometimes five-jointed, probably varying according to the species. Unlike the mouth-parts of most diptera, those of *Culex*, with one exception, are free to the base; this exception is that the labrum and epipharynx are united their whole length, forming a piece, which is shown in section in fig. 6, *d*. The labium and palpi are the only mouth-parts which contain muscles. The epipharynx forms the channel through which *Culex* sucks up blood; the hypopharynx probably furnishes a channel for the discharge of a saliva-like fluid. A pumping organ, trianguloid in cross-section (fig. 10, *b*), for sucking up blood into the pharynx, is formed by a dilation of the oesophagus behind the oesophageal nerve-ring. Each of the above parts will be described more in detail later. In comparative size and strength the mouth-parts would be arranged as follows, the largest and stoutest first: labium, labrum-epipharynx (the name by which I shall designate this compound piece), hypopharynx, maxillae, and mandibles.

The general arrangement of the mouth-parts, relative to each other, is shown best in fig. 8, which is of a cross-section through the middle of the proboscis of a female *Culex rufus*, while in repose, with the setae sheathed in the labium. The labium (*l*), clothed on the outer side with its scales and hairs, wraps itself nearly around the other mouth-parts. In it lay the two maxillae (*mx*), partly enclosing the parts above them, and thus helping to bind the parts together; above the maxillae are the two mandibles (*m*), and immediately above the mandibles, in a median line, is the hypopharynx (*h*), with a thickened middle portion. Resting on the hypopharynx is the labrum-epipharynx (*lr* and *e*); the epipharynx is omega-form in section, and above it, delicately attached, is the labrum. The determination of the positions of the hypopharynx, mandibles and maxillae, in a section, is difficult, because of their minuteness and transparency, and because that they are very closely packed together, much more closely, relatively, than they are represented in figure 8. Their position was finally determined by the following process, which I repeated several times to insure accuracy. The section of the proboscis, still in the parrafine in which it was cut, was put on a microscopic slide, covered with a cover-glass, and a piece of blotting-paper laid at that side of the cover-glass toward which the labium was turned. Then, while watching the parts carefully with the microscope, turpentine was passed under the cover-glass, at the side opposite the blotting paper, and allowed to flow slowly about the object until it

was imbibed by the paper at the other side. Thus a constant stream of turpentine flowed against the upper side of the mouth-parts, and they were dissolved away, in the field of the microscope, one after the other, in the order, labrum-epipharynx, hypopharynx, etc. The position of the parts can be also determined by pressing the head of *Culex* laterally between a cover-glass and a slide; in perhaps one case out of every twenty tried, the parts will arrange themselves as they did in the specimen from which fig. 1 was drawn. The changes in position which the mouth-parts of *Culex* undergo as they approach the head can be best described in the subsequent description, in detail, of each separate part.

The labrum-epipharynx (figs. 1, 5, 6, 7-8; *lr* and *e*) of *Culex* consists of the thin labrum resting upon and fastened to the epipharynx; it tapers gradually from base to apex. The epipharynx is omega-form, being a channel rather than a tube, a tube being formed by the pressing of the hypopharynx upon its under side. The tube thus formed is the channel through which the blood, which *Culex* sucks, passes into the oesophagus. At its base or proximal end the epipharynx is supported and moved by strong muscles having their insertions on the upper side of its wings or lateral portions, and upon the upper side of its tube. These muscles extend upward and posteriorly, and have their origin on the inner surface of the clypeus. (See fig. 9 and 11.) These muscles (*pm*) by their contraction, elevate, and perhaps slightly retract, the epipharynx, and the labrum, to which they are also attached. These muscles probably *aid* in suction, for, when the setae are all stuck firmly in the skin, the contraction of these muscles would only serve to raise the base of the epipharynx from that of the hypopharynx; this action would tend to produce a vacuum between the two (see fig. 9), and thus cause the blood to be drawn up in the tube of the epipharynx. The probability that these muscles aid in suction is augmented by the fact that the corresponding muscles in other flies, which cannot raise their epipharynx so freely from their other mouth-parts as is seen in fig. 1, these muscles are devoted to suction; and further, that in the male *Culex*, which does not possess — as does the female — a pumping apparatus behind the oesophageal nerve-ring, these muscles are the ones that must serve for suction. The section, represented in fig. 9, was taken near the base of the clypeus; a few sections further on, posteriorly, the channel for the passage of food turns upward and then backward again, passing in its course a place (fig. 11, *v*) where its walls approximate dorsally and ventrally. This narrowing of the walls is probably a valve to prevent the return of fluids to the mouth during the pumping process. I term the portion in which this sucking process is carried on, the portion of the tube which is between the mouth (where the mouth-parts unite to form a closed tube), and

this valve, the pharynx; posterior to this valve, oesophagus. These limitations of the oesophageal region will be found convenient later, when I compare the mouth-parts and the sucking pharynx of *Culex* with those of other diptera.

The tip of the labrum-epipharynx seems to turn upward (fig. 1, *lr-e*), altho the opening is upon the ventral surface, as may be seen in fig. 6, *b*, which represents the ventral view of the tip of this part. The tip of the labrum-epipharynx is comparable to a quill-pen with three tips near each other, the middle one of these three tips being slightly shorter than the other two. The two lateral portions of the epipharynx, as seen in section, when they near the tip, lay themselves closely upon the sides of the tubular portion, passing upward upon it, as seen in fig. 5, *lr-e*; they thus serve to strengthen the two outer points of the tip of the epipharynx, while the labrum continues to a sharp point at the tip, and, united with the upper surface of the epipharynx tube, forms the middle point of the tip. The channel, or slit, along the under side of the epipharynx, widens toward the tip, leaving thus an opening for the passage of fluids into the tube of the epipharynx.

The labrum itself is a thin lanceolate lamella of chitin, concave along the under side from the basal portion to the tip, and its concavity rests upon and fits to the convexity of the tubular part of the epipharynx, to which it is so lightly attached that they readily separate by application of caustic potash. The outer edges of the labrum roll slightly inward toward the epipharynx along most of its length. (See fig. 6, *d*.) At its base the labrum sends a chitinous support beneath the clypeus, where it separates more from the epipharynx and has its own muscles, indicating that the labrum has a degree of motion independent of the epipharynx, a motion allowed, perhaps, by the elasticity of the connection between the labrum and epipharynx. The muscles of the labrum (fig. 9, *pm'*) are inserted upon the upper side of its base and have their origin on the inner surface of the roof of the clypeus. These muscles are, at least in the females of *Culex rufus*, divided into three portions in their upper part, as shown in fig. 9.

The hypopharynx of the female of *Culex* is a linear, lanceolate, transparent lamella of chitin, with a longitudinal rod through the middle, the nature of which will be discussed later. At its base the hypopharynx forms the continuation of the under wall of the pharynx. (See fig. 11, *h*.) The hypopharynx is closely pressed upon the under side of the epipharynx, completing the tube nearly formed by the epipharynx. No muscles have their insertion on the base of the hypopharynx. Its tip is simply lanceolate (fig. 5, *h*). In *Culex pipiens* and *C. rufus* nothing further is visible (with a magnifying power of five hundred diameters), in sections of the thicker middle portion of the hypopharynx, than a simple

rod of chitin; but, in *C. ciliatus*, a North American species of which the mouth-parts are larger, this rod appeared to be tubular. Is it a rod or is it a tube? Menzbier [8] writes (p. 25) that in diptera "neither the labrum nor the hypopharynx possesses a completed tube, but only a channel" * which leads into the salivary duct. That Menzbier is incorrect in affirming that the hypopharynx has no complete tube I have clearly proved in my observations on *Bombylius* and *Eristalis*; but the question still remains unsettled whether *Culex* has any passage, either tube or groove, through the hypopharynx. Réaumur[12] (tome 4, part 2, p. 396) discusses the probability of a poisonous fluid being secreted by *Culex*, to cause the blood to flow more readily when it bites, and since his time writers have, on the one hand, accepted this statement, without proving the presence of such a fluid or of the glands to secrete it, or they have, on the other hand, denied the existence of such a fluid, and affirmed, as Leeuwenhoek did, that the swelling subsequent to the bite of *Culex* was due to the irritation produced by the tearing of the mouth-parts in the skin, without the aid of a poisonous secretion. After having experimented a large number of times with the living mosquito, I am convinced that there is use made of a poisonous saliva; for, when biting, if the mosquito fails to strike blood, which it often does on parts of the back of my hand, it may have inserted its proboscis (labium of course excepted) nearly full length, in from one to six directions, in the same place and withdrawn its proboscis; indeed it may have inserted its proboscis, as often occurs, in extremely sensitive parts; yet in such cases, if no blood be drawn, no more effect is produced upon my skin than is produced by the prick of a sharp needle; a red point appears only to disappear in a few hours. Certainly there has been as much tearing of tissues in such a case as the above-mentioned, as there is when *Culex* settles on a place richer in blood, and, with a single probing, draws its fill. When the insect is allowed to draw its fill on the back of my hand, the subsequent swelling lasts from forty to forty-eight hours, and the amount of poisonous effect upon me, as proved by numerous experiments, is in direct proportion to the length of time which the *Culex* has occupied in actually drawing blood. The above-mentioned facts would indicate a constant outpouring of some sort of poisonous fluid during the blood-sucking process, and would necessitate a tube or channel for its conduction. Now no other channel exists through which saliva could pass from the base to the tip in the mouth-parts which *Culex* inserts in the skin, and this, together with the position occupied by the

* "Dass weder das Labrum noch die Hypopharynx eine vollständige Röhre besitzt, sondern nur einen Kanal."

salivary duct in other diptera, leads me to believe, without as yet being able to give anatomical proof of it, that the hypopharynx of *Culex* contains a duct that pours out its poisonous saliva. Not having fresh specimens of *Culex ciliatus*, and the extreme minuteness of the hypopharynx in the species of *Culex* available, has precluded my determination of the actual presence of glands in connection with this mouth-part.

The mandibles (figs. 1 and 8, *m*), the most delicate of the mouth-parts of *Culex*, are two very thin linear-lanceolate lamellae of transparent chitin, which rest with their inner edges beneath each half of the hypopharynx, their outer edges projecting beyond its outer edge, on each side. The mandibles are so thin and transparent, and so tightly pressed upon both the hypopharynx above and the maxillae below, that they easily remain undiscovered in sections of the proboscis. At the base of the proboscis they appear to have no muscular attachments, but to lie imbedded in the connective tissue, beneath the pharynx and above the maxillae. (See fig. 9.) They are slightly tapering from the base to the tip, but are of equal thickness throughout their breadth; at the tip they have a slight thickening, in form of a letter V, with its opening turned toward their very delicate, almost invisible tip. (See fig. 5, *m*.)

The maxillae (mistaken by Gerstfeldt * for the mandibles), are tapering lamellae of chitin, apparently serrate at the tips. Each maxilla is thicker near the inner edge, the thickening being formed by a solid chitinous shaft, which is fixed longitudinally upon the upper side. (See fig. 5 and 8, *mx*.) The bases of the maxillae join the stouter maxillary palpi just before passing under the clypeus, and immediately afterwards they join the labium, and become imbedded, with the mandibles, in connective tissue. (See fig. 9, *mx*.) Their continuations in the head are two delicate chitin-supports, each of which ends in a strong muscle; this muscle, the retractor maxillae (fig. 10, *rm*), passes backward and downward through the head, beneath the infraoesophageal ganglion, and has its origin in the posterior basal part of the head. The maxillae probably have no protractor muscle, their forward motion being due to the elasticity of the chitin frame-work of the head. The shaft of the maxillae is very transparent, except near the inner side where the chitin-rod runs; here it is brownish and more opaque. Out from the above-mentioned chitin-rod extends a very delicate feathering, or corrugation, of chitin to the edge of the most transparent portion

* Gerstfeldt [3] (p. 33) says, "of which the mandibles, toothed at the end, are somewhat broader but of the same length as the toothless maxillae." In the original, "von welchen die am Ende gezähnten Mandibeln etwas breiter, aber ebenso lang als die zahnlosen Maxillen sind."

of each maxilla, as seen upon the basal portion of fig. 5, *mx*. In some species of *Culex* this feathering is right-angled with the direction of the chitin rod; in other species oblique-angled, with the angle pointing forward, so as to form a series of barblike corrugations. The tip of the maxillae (fig. 5, *mx*) is very acute, has none of the before-mentioned chitinous corrugations, but, in their place, near the outer edge, is a row of papillae, which have their tips slightly recurved toward the head, and consequently appear serrate. These papillae are different in number in different species, and probably in different individuals of the same species. That they are true papillae, and not points of a serrate edge, is not always at first apparent, but becomes so by observing them in all directions, and is still further shown, in certain species of *Culex*, where they are situated near the middle of the blade of the maxilla. These papillae are upon the upper surface of the maxillae, as can be readily seen, by preparing the mouth-parts by lateral pressure, as in fig. 1.

The maxillary palpi (figs. 1, 2, and 9, *mp.*) are four-jointed in some species of *Culex*, five-jointed in others. At first sight they appear to be three-jointed, but more careful examination serves to show that the apparent basal joint is made up of two joints, and oftentimes to reveal a very short, knob-like joint at the extremity of what appears to be, at first, the apical joint. At their base the maxillary palpi join the maxillae just before the latter pass beneath the clypeus, and, with the maxillae, join the other mouth-parts, as shown, in section, by fig. 9.

The function of the maxillae is, probably, to draw the other mouth-parts into the skin, when *Culex* bites, for if one watches the maxillary palpi of *Culex*, while the setae are entering the skin, the setae seem to pierce the skin, and enter it with a slow gliding motion, as if drawn from below, instead of pressed from above; meanwhile, if one observes carefully, with a lens, the maxillary palpi can be seen to be in an alternating motion, as if the maxillae to which they are attached, pressed, first one then the other, into the skin, and then pulled the other parts after them. The muscles, retractores maxillarum, already described, lend weight to this view of the functions of the barbed maxillae.

The labium (figs. 1, 2, and 3, *l*), the largest of the mouth-parts of *Culex*, and the only one of them, helping form the proboscis, which contains muscles, forms a sheath opening along the upper side, and receiving in its channel the other mouth-parts (excepting the maxillary palpi), as seen in cross-section in fig. 8; it tapers from base to tip, is flexible, has a delicately annulated structure, and is clothed with hair and scales. At its base it unites with the maxillae, mandibles, and hypopharynx, and continues into the under surface of the head. Throughout its length it contains, on each side, muscles, which have their origin

in the base of the head and serve to control the motions of the labium. (See figs. 8 and 9, *ml.*) At the sides of the tip of the labium are attached two lobiform appendages, the labellae, which are seen at *lb* in fig. 3 with the true tip of the labium proper between them. These terminal lobes are jointed to the labium, a little distance behind its tip, as can be seen in fig. 7, which is a cross-section of the labium a trifle anterior to the actual centre of motion of these joints. The section of that portion of the labium which extends forward to form its tip is seen in the middle of the figure, just below the section of the maxillae (*mx*). Outside the section of each lobe is seen the section of the exterior edge of the labium itself, which here forms a double socket, or pair of acetabula, into which the heads of the two labellae are set. The reason why this exterior edge of the labium does not appear, in the section, as entirely surrounding the sections of the labellae, is that the labium extends forward further on the dorsal and ventral sides than at other points. Each of the lobes of the labium, — the labellae, — is provided with an extensor and flexor muscle. (See fig. 7, *me,* and *mf.*) The extensor muscles (*me*) are toward the outer side of the cavity of each lobe, and serve, when simultaneously contracted, to separate the tips of the labellae; the flexors (*mf*) are upon the inner sides of the cavity of each lobe, and serve to approximate the tips of the labellae. Near each flexor is to be seen (fig. 7) the section of the thickening of the chitin-walls, which, continued as a chitinous rod, extends a distance back into the labium, and serves as attachment for the flexor. In *Culex*, then, the labellae are attached to the labium by true joints.

The labium has for function, for the most part, the protection of the fine setae which form the true piercing organ of *Culex*. In the females of *Culex* proper, the protective sheath is formed by the labium alone. When the mosquito has found a place which suits its taste for piercing — for it often tries different places on our skin with its labellae, probing right and left, before finding a place where it decides to remain — it plants its labellae firmly upon the spot, and a moment later the labium is seen to be flexing backward in its middle, the setae, firmly grouped together, remain straight and enter the skin, while the two labellae guide them, much as a carpenter guides his bit with his fingers, while boring a piece of plank. When the setae of *Culex* have entered the skin to nearly their full length the labium is bent double beneath the body of the insect, the labellae still holding the base of the setae at the point where they enter the skin. When the mosquito wishes to withdraw the setae it probably first withdraws the two barbed maxillae beyond the other setae, that is, so that their barbs, or papillae, will be kept out of action by the mandibles and hypopharynx; then it readily withdraws the setae, perhaps aiding their withdrawal by the

muscles of the labium, for, during the process of extracting the setae from the skin, while they are slowly sinking back into the groove upon the upper side of the straightening labium, the mosquito keeps the labellae pressed firmly upon the skin. Réaumur described carefully, in his memoir, the process of biting in *Culex*, and was the first, probably, to describe and figure how the insect disposed of its labium during the operation.

The mouth-parts of *Culex*, as above described, are suspended under a clypeus, or epistom, which is figured from the side in fig. 1, *c*; from above in fig. 2, *c*; in length-section in fig. 11, *c*; and in cross-section in fig. 9, *c*. This clypeus is the hood-shaped forward continuation of the lower part of a Λ-shaped piece of chitin which forms the framework of what may be termed the "face" of *Culex*; right and left of the upper portion of this framework pass out the antennal nerves, the antennae being supported by the framework itself.

The pharynx (fig. 11, *p*), the tubular continuation of the epipharynx above and the hypopharynx below, as it passes backward, beneath the centre of the Λ-shaped framework, turns somewhat upward, is narrowed to the valve previously described, then widens slightly again, and, as oesophagus (fig. 11, *oe*) passes through the oesophageal nerve-ring, in which it is supported by three delicate chitinous rods, which lay, one longitudinally on its ventral surface, and two to the right and left on its dorsal surface. Just posterior to the oesophageal nerve-ring, directly above the nerve-commissure which connects the infraoesophageal ganglion with the first thoracic ganglion, the oesophagus suddenly expands into an oesophageal pump, or bulb, the longitudinal section of which is shown in fig. 11, *b*; the cross-section in fig. 10, *b*. This bulb, which is the chief sucking organ in the female *Culex*, is supported by three longitudinal chitinous rods, which are stouter continuations of the three rods supporting the oesophagus through the nerve-ring. These rods (fig. 10, *r*) have between them chitin-plates (fig. 10, *t*) which are suspended from the rods by elastic membranes. On the dorsal plate is inserted a double muscle, or a pair of muscles (*bm*), the origin of which is in the dorsal part of the chitinous shell of the head. Each of the lateral plates has inserted on it a muscle (*bm'*), the origin of which is in the chitin of the lower lateral regions of the head. The origin of each of these muscles is in the so-called occipital region of the head, that is, behind the eyes. By the simultaneous contraction of these muscles (*bm* and *bm'*), the lumen of the oesophageal bulb is enlarged, and the blood flows into the bulb from the pharynx, and, upon their relaxation, the elasticity of the chitinous walls of the bulb drives the blood, which cannot return to the pharynx because of the closing of the valve at *v* (fig. 11), into the stomach.

THE MOUTH-PARTS OF *CULEX*, MALE.

The mouth-parts of the male of *Culex* have not been described, as far as I know, with any degree of accuracy, altho, since Swammerdamm's time, the males have been distinguished from the females, by all scientific entomological writers on the subject, by means of their feather-like antennae and maxillary palpi. Jörgens[18] (Bd. 1, p. 165) thinks, contrary to the opinion of most writers, that the male mosquito can bite, and writes "But since the male is also provided with a sucking seta, it is not comprehensible why it should not use it for the same purpose." * He describes (p. 162), however, the setae of the male *Culex* as four in number, the same as he describes those of the female.

The proboscis of the male of *Culex pipiens*, the only species the male of which I have studied, is slightly longer and slenderer than the corresponding organ in the female. The five-jointed maxillary palpi are covered with long hair at the tip. The setae are fewer in number and less completely sheathed by the labium than in the female; they consist of a well-developed labrum-epipharynx and two slightly developed maxillae. The mandibles are absent, and the hypopharynx coalesces with the labium (fig. 12, *h* and *l*). The labium and maxillary palpi are more densely covered with hair and scales than they are in the females, and they contain muscles; the other mouth-parts, the setae proper, are naked, chitinous, and contain no muscles. In comparative length the mouth-parts may be arranged, longest first: maxillary palpi, labium and labrum-epipharynx, maxillae; — in comparative size they may be arranged, largest first: labium, maxillary palpi, labrum-epipharynx, maxillae. The relative position of the mouth-parts of the male, determined in the same way as for the female, is different from that in the female (compare fig. 8-9 with 13-15) in that the short, rudimentary maxillae are pushed out sidewise to allow the hypopharynx to coalesce with the labium. In the male the oesophageal pump, or bulb, behind the nerve-ring fails, and the sucking of fluids must be done by the pharynx alone, as it is done in most diptera.

The labrum-epipharynx is nearly the same in general form and structure in the male *Culex* as it is in the female, it is a trifle longer and slenderer, but the same figures (5 *lr-e*, and 6) will serve for the tips of both. In section (fig. 12, *lr-e*), the labrum shows a groove on its upper surface, which deepens as it nears the base (fig. 13, *lr-e*). At its base the labrum-epipharynx unites with the

* "Da aber auch die männliche mit eben dem Saugstachel versehen ist, so ist nicht einzusehen, warum sie sich desselben nicht zu gleicher Absicht bedienen sollte."

maxillae and their palpi before it unites with the labium, as shown by fig. 14. The apical four-fifths of the labium contains no other seta than the labrum-epipharynx, as seen in fig. 12, which is a section at about the middle of the proboscis. At the base of the labrum-epipharynx are inserted pharyngeal muscles similar to those found in the female, and with similar insertions and origins, except that the median muscle (fig. 15 *pm'*) is not divided into three parts as in the female (fig. 9, *pm'*).

The hypopharynx is, throughout its whole length, joined to the labium, and thus necessarily pushes the maxillae, which would normally lay between it and the labium, to one side. (See fig. 13, *h* and *mx*.) The hypopharynx shows, in section (fig. 13-15 *h*), the same chitinous rod through the middle as in the females, but I was unable to detect any channel for saliva through this rod.

The maxillae are very thin lamellae of transparent chitin, about one fifth as long as the labium, and so delicate as to be easily overlooked. Altho as broad at the base as is the tube of the epipharynx, they taper regularly from their base to their fine tips. When the maxillary palpi are carefully pulled from the head of the male *Culex*, the maxillae usually remain attached to their base. The attachment of the maxillae to the maxillary palpi is readily seen in sections (fig. 13, *mx* and *mp*); that they are not mandibles is evident.

The maxillary palpi are five-jointed, very hairy toward the tip, much longer than they are in the female, and when at rest their basal portions cover the labrum-epipharynx and maxillae in the sheath of the labium.

The labium of the male *Culex* is similar in general structure to that of the female, if one considers it together with the hypopharynx. It is, however, slenderer, more densely covered with scales, has a shallower groove for the reception of the labrum-epipharynx, and has a joint near the middle. The slenderness of the labium in the male extends itself to the labellae. (Compare fig. 4, *lb* with fig. 3, *lb*.) The groove of the labium of the male increases in shallowness from tip to base; at the middle of the proboscis (fig. 12) it is so shallow that it fails to fully protect the labrum epipharynx, and at its base (fig. 13) it is so shallow that the other mouth-parts rest only on top of the labium. To make up for this deficiency of protection by the labium, the maxillary palpi, as was previously mentioned, cover over the upper side of the enclosed parts (see fig. 13), and thus, altho free from the labium, form a part of the protective sheath, which, in the female, is formed by the labium alone. Whether the joint near the middle of the labium of the male *Culex* is true or false I cannot say, since I have never seen it bent by the insect itself; its appearance is that of a true joint. Like the labium of the female, that of the

male has two longitudinal main tracheal stems (figs. 12-14, *tr*), and two rows of longitudinal muscles.

Whether the male *Culex* can bite, or not, is a question to which I can give no decisive answer; but I do not believe it can. I have tried to have the male mosquitos bite me when in the field, where they were abundant, but they did not seem attracted, as the female mosquitos were, to my person; they flew away indifferently without lighting upon me. I have often taken male mosquitos, with all possible care to prevent disturbing them, beneath a glass cover upon my hand, letting them remain long enough to be as tranquil as they were when upon the leaves and grass of the field, but they would neither bite nor show any desire to do so, nor have I been able to feed male mosquitos with water, saliva or fresh blood, all of which liquids the females often drink with avidity.

Upon anatomical grounds I believe that male mosquitos take liquid food, altho I have never dissected their stomachs to see what this food was. They have mouth-parts and pharynx developed sufficiently to suck liquids; but the absence of barbed maxillae, of a free hypopharynx, and of an oesophageal bulb, leads one to suppose that they take a smaller quantity of food than the females do, and that they do not obtain it by piercing the skins of animals.

THE ANATOMY OF THE MOUTH-PARTS OF *BOMBYLIUS*.

The mouth-parts of the *Bombyliidae* have been studied only superficially. Sulzer[14] says (p. 174) "The proboscis" of *Bombylius* "is as long as and longer than the thorax, extended horizontally, bristle-like, more flexible apically, and is only the sheath for the true sucking-seta, which comes out through its upper side, which, as in *Conops*, is split longitudinally." * Fabricius writes (*Syst. entom.*, p. 802), "Mouth haustellate, without proboscis. Haustellum very long, straight, setaceous, bivalvate" ** and (*Phil. entom.*, p. 50), "setae three." *** Gerstfeldt[3] writes (p. 31-32), "The *Bombyliidae* also have four setae, which always represent the maxillae, the upper lip and the hypopharynx, while the mandibles are united with the proboscis-sheath — in *Bombylius* the hypopharynx

* "Der Rüssel ist so lang, und länger, als die Brust, horizontal ausgestrekt, borstenähnlich, vorne biegsamer, und nur die Scheide zu dem rechten Saugstachel, welcher durch die obere Seite, die, wie bei dem Pferdstecher, der Länge nach gespalten ist, heraus kömmt."

** "Os haustellum absque proboscide. Haustellum longissimum, rectum, setaceum, bivalve."

*** "Setae tres."

exceeds the upper lip in length, and the maxillae are still shorter than the latter; all the setae appear hard and sharp." *

The species of *Bombyliidae* which I have chosen for study is *Bombylius major*. Its proboscis is about three times the length of its head (See Pl. 2, figs. 1 and 2), and extends directly forward from the ventral side of the anterior portion of its head, in such a position as to be parallel with any plane on which it alights. Gerstfeldt[3] (p. 14) incorrectly regards the proboscis of *Bombylius* as extending first directly downward, and then bending, knee-formed, forward. The pharynx at the entrance of the head, turns slightly upward (fig. 3, *p*), but the proboscis itself is straight. The tip of the proboscis is divided into two labellae, which separate and press themselves, with a rubbing motion, upon whatever *Bombylius* eats. When the labellae are separated the tip of the hypopharynx is visible (as in fig. 2) between them. The basal half of the proboscis often appears split into an upper and under portion. At each side of the base of the proboscis arises a one-jointed palpus, at the base of which the maxilla can be seen (fig. 1, *mx*) to pass downward and into the side of the proboscis, between the above-mentioned upper and under portions. The different parts of the proboscis can be separated from one another with dissecting needles, and are five in number, but their determination, as regards length, position, and homology, is better revealed by sections, a series of which (fig. 1, α-λ') are connected by dotted lines to the place in the figure of the proboscis and its base, from which the sections, which are represented in the figures, were taken. As shown by these sections the mouth-parts consist of three unpaired organs, labrum-epipharynx, hypopharynx, and labium, and of a pair of maxillae with maxillary palpi at their bases. These parts will be described in detail further on. The comparative length and size of the separated labrum-epipharynx, hypopharynx, and maxillae, can be seen in the upper portion of fig. 1, where they are represented in their proportionate lengths and sizes, as compared with the entire proboscis figured below them. All the mouth-parts of *Bombylius* are without articulations and are more or less pubescent, altho the hairs are very minute on the maxillae. (See fig. 4.) When at rest the organs of the proboscis are thus arranged (Compare fig. 1, η and ϑ): the hypopharynx (*h*) lays in a groove on the upper side of the labium (*l*) and is covered by the labrum-epipharynx; beneath or at the side of the labrum-epipharynx (*lr-e*) are the maxillae (*mx*) and maxillary palpi (*mp*).

* "Vier Borsten — die immer den Maxillen, der Oberlippe und dem hypopharynx entsprechen, während die Mandibeln mit der Rüsselscheide verschmolzen sind — besitzen auch die *Bombyliarien* (bei *Bombylius* übertrifft der hypopharynx die Oberlippe an Länge und die Maxillen sind noch kürzer als letztere, alle Borsten aber erscheinen hart und spitz)."

The labrum-epipharynx (seen in cross-section in fig. 1, *β-ι*, *lr-e*; from beneath in fig. 1, *lr-e*) is composed of the labrum, which is a direct continuation of the front walls of the head, and of the epipharynx, which is a direct continuation of the upper chitinous lining of the pharynx. These two parts (fig. 1, *ϑ*, *lr* and *e*) are so combined that the upper convex surface of the epipharynx fits into the under concave surface of the labrum, while the edges of the epipharynx are connected to those of the labrum by a less strongly chitinized membrane, whose infolding between the two can be distinctly seen on sections *ε-ι*. The enclosed space between the labrum and epipharynx contains longitudinal muscles, tracheae, and connective tissue. The muscles are at each side of the tube of the epipharynx, and are represented in cross-section on fig. 1, *η-ι*. Below the muscles on each side, near the fold between the labrum and epipharynx, is a tracheal stem, seen in cross-section in sections *ζ-κ*. The combined labrum-epipharynx tapers from base to tip, is shorter than the hypopharynx and labium, but longer than the maxillae. Of its two component parts the labrum undergoes much more change in form, from base to tip, than does the epipharynx. The epipharynx forms a channel, open along the under side by a narrow slit; this slit widens as it approaches the tip, and bears on its two sides hairs, pointing inward and backward, to prevent the return of food (See fig. 1, *lr-e*); for it is through the epipharynx, as in all diptera which I have studied, that the food passes. At its basis the labrum-epipharynx, by a sort of reflexion of its margins, forms chitin-plates, which serve to support it in the forward part of the head (see fig. 1, *λ'*), and to contain the pharyngeal muscles (fig. 1, *λ'*, *pm* and fig. 3, *pm*), which elevate the upper elastic wall of the pharynx, in the action of sucking. As will be seen later, in the portion of this paper which I devote to the comparison of the parts of the different species studied, this reflexed wall of the pharynx is the homolog of the greater part of the so-called fulcrum of the *Muscidae*.

The hypopharynx of *Bombylius* is a flexible tube of thin chitinous membrane, containing within itself a more rigid chitinous tube, which opens on the upper side near the extremity of the hypopharynx. The tip of the latter is thus of the form of a pen, with its concave side upward. (See fig. 1, *h*.) The inner tube of the hypopharynx is continuous at its base with the salivary duct; the outer flexible tube only serves to make the hypopharynx fit more closely to the form of the surrounding mouth-parts. The upper surface of the hypopharynx is naked; its lower surface hairy. Its section (fig. 1, *η* and *ϑ*, *h*) is variable in form on account of the flexibility of its outer tube. Just before it reaches the mouth, that is just before it unites with the epipharynx to form the mouth, the hypopharynx joins, on each side, with folds from the united maxillae and maxillary

palpi. (See fig. 1, *x*.) The tip of the epipharynx rests between the labellae, as is seen in fig. 1, *α*, and in fig. 2.

The maxillae (fig. 1, *mx*) are slender, solid, chitinous rods, the outer or apical halves of which lay along each side of the hypopharynx; their basal portions pass more and more outward, so that their bases are at each side of the labrum-epipharynx. (See fig, 1, *ϑ*, *mx*.) In cross-section the maxillae are reniform, with the concave sides inward, gradually changing to triangular towards their tips, where their outer sides are very finely and densely pubescent. (fig. 4.) Between the portions represented in sections *ϑ* and *ι*, the maxillae are joined by the maxillary palpi, and, at about the same time, they join a fold (*l'*) of the labium, which fold, as seen in section, surrounds the labium itself. The bases of the maxillae (*x*) extend deep into the head.

The maxillary palpi (fig. 1, *mp*) are slender, hairy, cylindrical, and lay just outside, and at the base of the proboscis. Their bases lay at the sides of the labrum-epipharynx; their tips usually directly over it.

The labium (fig. 1, *l*) is slender, hairy, and its outer fifth is divided into two labellae. Throughout its length, the labellae excepted, the labium forms a channel (see sections *γ*-*ι*) for the reception of the hypopharynx and maxillae. It contains two longitudinal tracheal stems, and longitudinal muscles; it is especially flexible toward the tip. At its base the upper surface of the labium joins the under surface of the hypopharynx, and its under surface continues, with two folds (*l'* and *l''* of figs. 1, *ι*-*x*, and of fig. 3), directly into the lower surface of the head. The labellae are not jointed to the tip of the labium by a true joint, as in *Culex*, but are the continuations of the two lateral halves of the labium. The tip of the labium projects between them, however, as can be seen in section *β*, where the cross-section of the tip of the labium is shown, at its first point of connection with, and between the two labellae. Each labella contains a flexor and extensor muscle, the flexor a little above the extensor in position. The labellae are usually pressed closely together, but can be separated, as seen in fig. 2, or even wider, so as to be at right angles to the axis of the proboscis. On the inner side of each labella are three longitudinal grooves or channels, held open by semi-rings of chitin at right angles to their axes, and toothed on each side. These, on account of their general resemblance to tracheae, were termed by Suffolk[21] pseudotracheae, in his description of them as they appear in *Musca vomitoria*. These pseudotracheae are seen in section in fig. 1, *α*. Fig. 5, *a*, is a perspective view of the pseudotracheae of *Bombylius major*, when at rest, with their teeth turned inward (fig. 6, *a* is cross-section of the same); fig. 5, *b*, shows

them in perspective, when *Bombylius* is feeding, with their teeth turned outward (fig. 6, *b*, is a cross-section of the same).

The functions and finer structure of these pseudotracheae, together with other points in the anatomy of the mouth-parts of *Bombylius*, will be further discussed in the part of this paper devoted to a comparative study of the mouth-parts of different diptera.

ANATOMY OF THE MOUTH-PARTS OF *ERISTALIS*.

Little has been done in the study of the anatomy of the mouth-parts of *Syrphidae*, of which I have chosen *Eristalis horticola* for anatomical investigation. Gerstfeldt[3] (p. 28-29) gives a general description of the mouth-parts of the *Syrphidae*, which can be condensed as follows: labrum blunt, with the tip separated into several points; hypopharynx always present; mandibles more or less rudimentary and coalesced with the sheath of the proboscis; maxillae fairly well developed and setiform; labium with well-developed terminal lobes. Menzbier[8] (p. 57-60) describes the proboscis of *Syrphus taeniatus*. His results, as regards the typical structure of the mouth-parts of *Syrphus*, may be summarized thus: labrum and epipharynx united; hypopharynx with a channel for salivary secretion; mandibles present; only remnants of the maxillae are the two maxillary palpi; labium with well developed terminal lobes. Menzbier, in describing the proboscis of *Syrphidae*, divides it into three portions, a basal, a middle, and a terminal portion. Leaving all reasons for my own views to be given in detail later, I will only say here, that this division of the proboscis of the *Syrphidae*, *Muscidae*, and other families of diptera, into basal, middle, and terminal portions, has served to render the study of the mouth-parts of these insects more complex and more difficult than it would otherwise be, and that, while retaining the term basal portion, for reasons to be given later, as a convenient designation for a part of the proboscis, I lay little value on such a division of parts. The so-called middle and terminal portions of the proboscis of the *Syrphidae* and *Muscidae* are really a single portion.

The proboscis of *Eristalis horticola* (side view in Pl. 3, fig. 1) is hung upon the under side of the head, and, unlike the proboscis of *Culex* or of *Bombylius*, is extensible and retractible. When extended the proboscis of *E. horticola* is as long as the head, and points nearly directly perpendicular toward the surface on which the insect is resting. Its retraction is accomplished by means of joints, near the points indicated on the figures by *d* and *g*. If the retraction is begun, by a partial revolution toward the head, of the portion of the proboscis between *d* and *g*, around the extremity *d* as axis, then the end *g* will follow the course

represented by the dotted segment of a circle *gn*; and if, during the time that the above mentioned revolution is progressing, a revolution of the portion of the proboscis *gk* around the axis *g* takes place, then the tip of the proboscis, *k*, will follow the direction indicated by the paraboloid curve *kd*. When these two partial revolutions, around the axes of the joints at *d* and *g*, are completed, as far as possible, the points *g* and *n*, and *k* and *d*, will have been closely approximated, and the proboscis will have been folded upon itself by a fold near its middle point, and, folded thus, the whole proboscis will have been retracted into a groove on the under side of the head. When fully retracted the dorsal * portion of the basal half of the proboscis is closely pressed against the dorsal portion of its distal half. Fig. 2 represents a longitudinal section of the head of *Eristalis horticola* with the basal half of the proboscis wholly retracted, and its distal half partly retracted. A section through the distal half of the proboscis of *Eristalis* (Fig. 1, β') shows all its mouth-parts in their normal positions. They consist of a labrum-epipharynx (*lr-e*), closed beneath by a hypopharynx (*h*). To each side of the above named parts lay the only paired mouth-parts, the maxillae (*mx*) and their palpi (*mp*). Beneath these parts the labium forms a channel for all the other mouth-parts, a channel into which they fit when the proboscis is retracted. No mandibles are present. A section through the proximal half of the proboscis (fig. 1, δ') shows none of the true mouth-parts. In the middle of this section is the channel for the passage of food, the pharynx (*p*), surrounded by the chitinous distal end of the so-called fulcrum, and its muscles (*pm*). At each side of the pharynx is a chitinous rod (*x*) which supports at its distal extremity the maxilla. Around these parts is a thin elastic membrane (*c l'*) which is continuous, proximally, with the chitinous covering of the head; and, distally, on the upper side, with the labrum, and on the under side with the lower walls of the labium. This elastic membrane, surrounding the forward extremity of the fulcrum, folds itself together, on the under side, between *n* and *g* (fig. 2), when the proboscis is retracted; on the upper side, when the proboscis is retracted, it receives in its folds the dorsal surface of the labrum.

The labrum-epipharynx is, in section (fig. 1, β' and γ', *lr-e*), nearly the shape of a horse-shoe, convex above, and is composed of the labrum, the continuation of the flexible walls of the upper side of the basal portion of the proboscis, and of the epipharynx, the continuation of the upper walls of the pharynx; but, in

* I shall use dorsal and ventral, upper and under, distal and proximal, and anterior and posterior, of the parts of the proboscis, in the same way and with the same meaning as if the proboscis were extended out from the front of the head.

Eristalis, the labrum and epipharynx are not connected, as in *Bombylius,* by infolding delicate membranes, to mark, in section, their line of union. The basal half of the labrum-epipharynx contains muscles passing obliquely upward and backwards from the epipharynx to the labrum; these muscles are only a forward continuation of the system of pharyngeal muscles in the fulcrum, which the base of the labrum-epipharynx joins. At its tip the labrum-epipharynx is divided into six parts, as seen in fig. 5, which represents the tip unrolled, from within, and these are hairy, the rest of the labrum-epipharynx being naked. The hairs on the inner side of the outer parts of the tip have the appearance of being sense-hairs, but I have only studied them superficially, and cannot therefore speak with certainty of their nature. The division of the tip of the labrum into several parts is regarded by Meigen[16] (Theil 3, p. 381) as a characteristic of the *Syrphidae,* and the researches of Gerstfeldt, as well as my own examination of the labrum of about a dozen species, tends to confirm Meigen's statement.

The hypopharynx (fig. 6; in cross-section, fig. 1, β' and γ', *h*) is lanceolate, naked, and strongly chitinized. It is a rigid tube, opening apically on the upper side, and is the outlet for the saliva. Its proximal end is slightly broadened, and unites, with a true joint, to the under walls of the distal end of the fulcrum, or pharynx. The margins toward the tip and the tip itself of the hypopharynx are transparent; the remainder of the hypopharynx is opake.

The maxillae (fig. 4, *mx,* and, in section, fig. 1, β', *mx*) are thin naked blades of chitin, concave on their inner sides, convex on their outer sides, and uniting at their bases with the maxillary palpi. The bases of the maxillae lay directly outside of the labrum-epipharynx, when the proboscis is extended, but the maxillae curve downward and inward, distally, so that their tips are between the hypopharynx and labium. The margins and tip of the maxillae are very transparent, the middle a little thickened. The maxillary palpi (fig. 4 *mp*; fig. 1, β', *mp*) are cylindrical, one-jointed, hairy, a trifle longer than the maxillae, and lay along the sides of the labrum-epipharynx, when the proboscis is extended (fig. 1). The chitinous supports which bear the maxillae at their tips, extend back along each side of the pharynx, where they can be seen, in section, at *x* in fig. 1, δ' and ε'.

In *Eristalis horticola* I was unable to find the least traces of the mandibles, either as free rudimentary structures, or as portions united to the labium. What Menzbier considered to be mandibles in *Syrphus taeniatus,* are, undoubtedly, maxillae. Menzbier[8] writes (p. 60) "At the sides of the basal portion of the labium and united with it, lay two thick chitinous structures, which project right

and left of the opening of the mouth in the form of three-cornered blades, or sharp prongs. These blades or prongs resemble so much the well-developed mandibles of chewing insects that we can rightly regard them as such. *Syrphus* has, then, besides labrum, epipharynx, hypopharynx and labium, a pair of mandibles. Near the mandibles, united with the basal portion of the proboscis, are two palpi. Since neither maxillae nor anything similar to them, are to be found on the mouth-parts of *Syrphus*, we must consider the aforesaid palpi to be the only remnants of the maxillae, since the latter always have palpi." * The above-quoted remarks give no valid reason for regarding the parts under consideration as mandibles, for the form which a part assumes in an animal has little value in determining its homology in comparison with the worth, in such determinations, of the position and attachments of the organ, the homology of which is in doubt; and, in this case, the situation of the maxillary palpi so near the base of the organs in question, together with the fact that the maxillae are present, and attached at the base to their palpi in *Eristalis* (fig. 4), leads me to suppose that the parts, which Menzbier regarded as mandibles in *Syrphus*, were really maxillae. This view is further supported by the figure ** which Menzbier gives, and by Gerstfeldt's statement that the mandibles are more or less rudimentary and united to the sheath of the proboscis, in the *Syrphidae*.

The labium of *Eristalis horticola* (side view in fig. 1; section in fig. 1, β' and γ', *l*) is larger than the other mouth-parts, muscular, pubescent on the outer or under side, and throughout its length run two tracheal stems and numerous longitudinal muscles. Its under surface and the middle of its upper side are strongly chitinized, but between these two portions the walls of the labium are very flexible, as can be seen in the sections β' and γ' of fig. 1. At its base the upper or inner surface of the labium joins the under side of the hypopharynx, at the point where the latter is jointed to the fulcrum; the under or outer surface of the labium passes (with a fold or two when the proboscis

* "An den Seiten des Basalkegels der Unterlippe und mit ihm verwachsen liegen zwei dicke Chitingebilde, die rechts und links von der Mundöffnung in Gestalt dreieckiger Schneiden oder scharfen Hacken vorspringen. Diese Klingen oder Hacken gleichen so sehr den wohlentwickelten Mandibeln der kauenden Insekten, dass wir mit vollem Rechte sie als solche deuten können. *Syrphus* besitzt also ausser Labrum, Epi- und Hypopharynx und Labium noch ein Paar Mandibeln. Neben den Mandibeln, mit dem Basalkegel verwachsen, sitzen zwei Palpen. Da weder Unterkiefer noch etwas ihnen ähnliches an den Mundtheilen von *Syrphus* zu finden ist, so müssen wir die erwähnten Palpen als einzige Reste der Unterkiefer betrachten, da Letztere immer Palpen besitzen."

** See Menzbier's pl. 3, fig. 3.

is not fully extended) directly into the under surface of the basal portion of the proboscis. On the upper side the labium is hollowed out to form a channel into which the labrum-epipharynx, hypopharynx and maxillae fit, when the proboscis is retracted, and usually when it is extended. To each side of the tip of the labium is attached a labella (in section in fig. 1, α'). The two labellae are short, fleshy, and hang below the level of the lower wall of the labium, often, when they are in use, seeming to be at an angle to it; thus they have more the appearance of distinct organs than they have in *Bombylius*. They are, however, nothing more than two hanging lateral wings of the labium, joined to it only by flexible chitinous walls, not by true joints. The labellae fold together so that the interior face of the one presses upon the interior face of the other, when they are not in use, and when the proboscis is folded in its channel beneath the insect's head. This seems to be the normal, or resting position, of the labellae, from which they are brought into action by a pair of extensor muscles, one in each labella (as seen in fig 1, α' in section); their further action will be described more fully later. Each labella has on its inner side pseudotracheae, all branching from a main pseudotracheal stem, which extends anteriorly and posteriorly along the upper side of each labella. The anterior portion of this pseudotracheal stem has about twenty-four branches, the posterior portion about eighteen branches. The branches of these pseudotracheal stems extend, approximately parallel to one another, from the upper to the under margin of each labella, and are much finer than, but of similar structure to, the pseudotracheae of *Bombylius*.

The structure of the so-called fulcrum, which occupies the central portion of the basal part of the proboscis, the use of the pseudotracheae, the mode of expanding the labellae, and other points pertaining to the structure and use of the proboscis in *Eristalis* will be discussed later, and more appropriately, in that part of this paper which will be devoted to a comparison of some of the corresponding organs in *Culex*, *Bombylius* and *Musca*.

ANATOMY OF THE MOUTH-PARTS OF *MUSCA*.

The proboscis of *Musca domestica*, the common house-fly, and that of *M. vomitoria*, the blow-fly, have attracted the attention of naturalists, from the time when Aristotle wrote, down to the present day, and to attempt anything like a complete notice of the different papers which, wholly or in part, treat, more or less fully, more or less scientifically, of this subject, would be an extravagant

expenditure of space and a waste of time. I select, therefore, for notice a few of the papers which treat upon the subject of the proboscis of *Musca*, or of its mouth-parts, such papers as seem to me to have furnished the more important contributions to our knowledge of the subject, or such papers as have so fully dealt with the subject that they ought not to be overlooked.

The earliest paper which I have thought worthy of notice here, that deals with the anatomy of the proboscis of *Musca*, is RÉAUMUR'S memoir [12] upon the trunks, with swollen and fleshy lips, which belong to two-winged flies.* This paper by Réaumur, — altho published in 1740, over thirty years before Fabricius had reduced the terminology of the oral organs of insects to anything like a system, and over seventy years before Savigny had settled the question that the mouth-parts of insects of all the different orders were homologous, — is a very complete and accurate presentation of many anatomical facts in regard to the proboscis of *Musca*. Réaumur, whose observations in regard to *Musca* were made, for the most part, on *M. vomitoria*, studied the proboscis, as was his usual method of study, with especial reference to its functions, and to the functions of each of its parts. Réaumur believed the proboscis of *Musca* to be essentially an organ for sucking, altho he thought that the food was aided, perhaps, by the undulatory motion which he observed in the proboscis, in its passage upward from the mouth, which was, according to him, between the two labellae. By watching a fly rolling a bit of dry sugar between the labellae, gradually moistening it, and thus slowly dissolving it away, Réaumur came to the conclusion that the fly had a salivary secretion, but, altho he describes the hypopharynx, by him termed the spur (*aiguillon*), as channeled above, he does not seem to have discovered that the channel of the hypopharynx was the outlet for the saliva. Réaumur correctly recognized the labrum-epipharynx as the part of the proboscis through which the food passes, and he therefore termed it the sucker (*suçoir*). He called the labellae lips (*lèvres*), and writes of them that they are traversed by, parallel channels, or flutes (*cannelures*), which extend toward the middle of the labellae; but, further on, he incorrectly assumes that this channeling is due to a large number of parallel vessels, which distend with liquid, when one presses the head of a fly, or when a fly wishes to use its labellae. Altho Réaumur does not directly say, in any place, that the proboscis of the fly is extended by means of injecting blood or air into it, yet the idea that the proboscis was extended by inflation was evidently often in his mind,

* Tome 4, part 1, p. 256-297, pl. 16-18. "Des trompes à lèvres grosses et charnues des mouches à deux ailes."

while writing about the proboscis, and he often uses the term inflate (*gonfler*) in regard to the proboscis or its parts. He writes (p. 259), "The fly can increase the volume of its trunk and can diminish it to a certain extent." * He further writes (p. 260), "One easily compels a fly to show its entire trunk, finely extended and well inflated; one has only to press between the two fingers the thorax, either laterally or from above and below; it seems as if one obliged the fly, immediately, to put out the tongue." ** Réaumur regarded the proboscis of *Musca* to be composed of, or folded into, two joints.

Gleichen,[22] in 1764 (p. 19-21), describes the proboscis of *Musca domestica*. He regards the proboscis as made up of three parts, longitudinally, namely a basal sac, a middle tube, and the proboscis proper, the latter being only the labellae. He writes (p. 19) that "The extension of the proboscis probably arises from the air, which is driven by the fly into the sac, and from this into the [middle] tube, finally into the lips. The elevation and depression of the proboscis is, however, brought about by the process with which the [middle] tube is supported." *** Gleichen writes further (p. 21), "The fly can indeed, as I have already mentioned, drive air between the membranes of the proboscis into the lips, but cannot take in air with them." †

Gleichen did not succeed in finding the part now known as hypopharynx in *Musca domestica*. He regarded the basal sac, or basal part of the proboscis, as a pumping organ.

Gerstfeldt's statements[8] (p. 24-26) regarding the mouth-parts of *Musca* may be noticed briefly as follows: the under lip, according to him, was what will be later described as labrum-epipharynx; his hypopharynx, as mentioned in the historical notes (p. 7) of this paper, was really the epipharynx, separated by the action of caustic potash, from the labrum; the real hypopharynx was not discovered by Gerstfeldt; the rudiments of the mandibles appear, according to Gerstfeldt, as the dorsal corner, on each side, of the fulcrum; the maxillae form

* "La Mouche peut augmenter le volume de sa trompe & le diminuer jusqu'à un certain point."

** "On force aisément une Mouche à montrer sa trompe toute entière, bien étendue & bien gonflée; on n'a qu'à presser entre deux doigts, soit les deux côtés, soit le dessus & le dessous du corcelet; il semble qu'on oblige sur le champ la Mouche à tirer la langue."

*** "Das Ausstrecken des Rüssels rühret vermuhtlich von der Luft her, die von der Fliege in das Säckchen, und von diesem in die Röhre, biss in die Lefze, getrieben wird. Das aufrichten und senken des Rüssels aber wird mit dem Hornbeinchen, womit die Röhre gefasset ist, bewirket."

† "Die Fliege kan zwar, wie ich bereits erwähnet, die Luft zwischen den Häuten des Rüssels in die Lefzen treiben, aber nicht damit Luft schöpfen."

the lateral portions of the fulcrum and support above the maxillary palpi; the labium, as submentum, mentum, etc., extends anteriorly from the base of the fulcrum and terminates in the labellae. Gerstfeldt's views of the homologies of the different parts of the fulcrum seem utterly untenable, as will appear later.

Lowne,[28] in 1870 (p. 41-51, pl. 2-3), describes and figures the proboscis and its parts in *Musca vomitoria*. He describes fully, and in general accurately, the fulcrum, which he regards to be homologous with the fulcrum of bees. The labrum-epipharynx, Lowne thinks, is composed of the labrum united with the terminal lobes of the maxillae, and he terms the organ as a whole the operculum, because it shuts like a lid over the other mouth-parts. Lowne correctly describes the hypopharynx under the name of tongue. The labium, which he calls the canula, is considered to be the united labium and mentum. I do not here go into further details in regard to Lowne's work, because I shall have occasion to notice it often in the following pages.

Macloskie, in 1880, describes the proboscis of the house-fly, *Musca domestica*, using for the most part Lowne's terminology, and discusses briefly several points about its homologies and functions. Among other things he again affirms the statement that inflation plays a prominent part in the extension of the proboscis; a statement criticized by Suffolk,[21] in 1869. Macloskie writes (p. 157-158), "It is easy to dispose of Mr. Suffolk's hasty criticism. Immerse the head of the fly in caustic potash, which destroys the muscles, the chitine of the membranous sheath and the tracheal tubes remaining intact, and you can still protrude the organ by slight pressure. Further, when the proboscis is pressed out and all its parts distended, pierce with a needle the swollen air sacs under the tip, and at once the tip collapses upon the mentum. If you tear the membrane about the base of the proboscis that part collapses. If you press the head over much, the membrane-sheath sends out bulging processes which soon burst, sending bubbles of air through the water in which you are examining it." I have verified the experiments mentioned by Macloskie above, besides trying others, and I think that an important factor in the cause of the extension of the proboscis of *Musca* is the injection of air into it. Macloskie also homologizes the fulcrum of the diptera with the endocranium of the cockroach (*Blatta*), a view that I am not prepared to affirm or to deny; but his conclusion that the so-called middle section is the true base of the proboscis, the so-called basal portion being a part of the head, and its organs internal, rather than true mouth-parts, this latter conclusion I hope to be able to prove in the concluding part of this paper.

Menzbier (p. 62-66) describes the organs which constitute the proboscis of *Musca*, and which are, according to him, the following: a labrum united to an

epipharynx, a hypopharynx, a labium, and two maxillary palpi; mandibles and maxillae are entirely absent. Menzbier says that the fulcrum is of "chitinized processes of the wall of the pharynx." * Menzbier criticizes severely (p. 26-27) several absurd statements made by Lowne, in regard to the proboscis of *Musca,* but says nothing further of Lowne's work, leaving one under the impression, if they depended for their information upon Menzbier's criticism, than Lowne's work was only a mass of absurdities.

Turning now from this brief historical summary of the progress of our knowledge of the mouth-parts of *Musca* to the results of my own studies, based almost wholly on the examination of the proboscis of *M. vomitoria,* I will describe briefly the proboscis and its parts in the above-named species, omitting many minutiae of structure, which it would be of little interest to mention in this connection, because they would have neither value in determining homologies or functions, nor use in the subsequent comparison of the mouth-parts of *Musca* with those of the other diptera which I have examined.

The proboscis of *Musca vomitoria* (side view of proboscis fig. 1, of pl. 4) is suspended from the under side of the head, and, like the corresponding organ of *Eristalis,* can be extended and retracted by means of joints. The general external aspect of the proboscis of *Musca* is like that of *Eristalis*; the mode of its folding by joints at the anterior under portion of the head and at the middle of the proboscis, is, in almost every respect, the same as it is in *Eristalis,* and need not be described here in detail. The most noticeable external difference between the proboscis of *Musca* and that of *Eristalis,* — a difference of limited morphological value, — which one sees in a hasty examination of these two diptera, is that the maxillary palpi of *Musca* are much larger, proportionally, than those of *Eristalis,* are inserted much nearer the base of the proboscis, and are borne much more erect from the proboscis, when the latter is extended, than they are in *Eristalis.* Another noteworthy difference in outward appearance, but not one of morphological worth, which is discovered between the proboscis of *Musca* and *Eristalis,* is that, in the former of the two genera, the labrum-epipharynx is never, by voluntary effort of the fly itself, extended above and free from the labium, so that one sees, in a side view (fig. 1) of the apical half of the proboscis of *Musca,* only the labium; while in a side view (pl. 3, fig. 1) of the same portion of the proboscis of *Eristalis,* one often sees the labrum-epipharynx, maxillae and labium.

A cross-section through the proboscis of *Musca,* made at the point indicated at α in fig. 1 and figured in fig. 1, α', exposes the labium (l) in the form of a

* "Chitinisirte Fortsätze der Schlundwand."

trough, in the hollow of which is the labrum-epipharynx (*lr-e*) with the hypopharynx (*h*) closely pressed beneath it. A cross-section of the same proboscis at β (figured in β'), fig. 1, reveals the bases of the maxillary palpi (*mp*) above, and within the proboscis a section of the distal half of the fulcrum, which contains the pharynx (*p*) and the pharyngeal muscles (*pm*). At each side of the pharynx is the section of a chitin-piece (*x*) and its surrounding muscle, the functions of both of which will be discussed later; directly beneath the pharynx, in the median line, the salivary duct (*sd*) is sectioned. If a section of the fulcrum be made still further toward its proximal end, its upper side will be found to be closed together, as in fig. 4.

The labrum-epipharynx of *Musca vomitoria* is a little longer than the hypopharynx, tapers gradually from base to tip, is strongly chitinized, is clothed with fine short hairs on the upper surface of its basal half, is in cross-section through the middle (fig. 1, α', *lr-e*) shaped like a horse-shoe with both its sides broadened, and is composed of a labrum and epipharynx, separable from each other in caustic potash. From the labrum to the epipharynx, in the basal half of the labrum-epipharynx, extend muscles. The extreme tip of the labrum-epipharynx has the shape of a quill-pen with its point evenly rounded off, is very thin and transparent, and is lined on its inner side with numerous very fine short spines. The base of the labrum-epipharynx is jointed to the distal end of the fulcrum in such a manner that the labrum is continuous with the upper surface (fig. 1, β', *c*) of the basal half of the proboscis, and the epipharynx with that portion of the fulcrum which directly covers the pharynx dorsally. The tip of the labrum-epipharynx is so completely surrounded by the sides of the labium, which, at the point where the labrum-epipharynx ends, are so developed dorsally as to form a tube, that the fly itself probably cannot raise the labrum-epipharynx out of the trough of the labium. The two can be separated, however, with a pair of needles without tearing the parts, if the operation is performed very carefully.

The hypopharynx of *Musca vomitoria* (fig. 1, α', *h*, in section) is thin, tapering gradually from its base to its tip, which is acute and sparsely clothed with very fine hair. The basal portion of the hypopharynx contains a tube, which opens into a groove on the upper side of the distal half of this organ; this tube is the outlet for the saliva, which is conducted to its basal end by a duct which has rings similar to those of tracheae. The course of this duct is shown by the dotted line *sd*, on figs. 2 and 3, and its position, in section, at *sd* of fig. 1, β'. The hypopharynx lays closely pressed to the under side of the epipharynx, from which it is not always easily separated, and with which it forms the tube for the passage of food to the pharynx. The base of the hypopharynx unites beneath

with the labium, somewhat anterior to the point where it joins the epipharynx above, to form the mouth.

Mandibles and maxillae, as free mouth-parts, are absent in *Musca vomitoria*. The one-jointed maxillary palpi (fig. 1, *mp*), two club-shaped appendages clothed with a few hairs, are attached to a slight thickening, or band, of the flexible membrane which bridges the upper anterior portion of the fulcrum. This band is marked by longer hairs than the rest of the membrane. The attachment of the maxillary palpi is shown on fig. 1, β'.

The labium of *Musca vomitoria* (side view in fig. 1; cross-section in fig. 1, α', *l*) is a deep trough or channel, the distal end of which is closed entirely over so as to form a tube; to the lateral margins of the distal end of this tube are attached the labellae. The walls of this trough (fig. 1, α', *l*) are double, that is, the trough itself can be compared to a cylinder of which the upper side has been so invaginated as to form a channel. These double walls extend into the tubular distal portion of the labium, so that the latter portion, structurally considered, is made up of one tube inside another, the greater part of the space between the tubes being beneath the inner one. The labellae are two lobiform hollow sacks; their inner margins are continuous with the inner tube above-mentioned, and their outer wall with the outer tube, so that their inner cavity, is, on each side, a continuation of the space between the two tubes. The basal channeled end of the labium is attached to the under side of the base of the hypopharynx above, and is continuous below with the lower half of the membranous sheath around the fulcrum. Through the labium extend stout muscles and two tracheal stems (fig. 1, α', *tr*). From the lateral edge of the inner chitinous tube, or wall, of the distal end of the labium there extends into the cavity of each labella a delicate curved chitinous band; on the bases of each of these bands are inserted muscles, which originate in the labium further toward its base. These muscles, altho not extending into the labellae, help to separate the latter from each other. The labium and labellae are somewhat hairy on the outer surface; especially is this true of the margin of the labellae. Each labella bears, on its inner surface, about thirty pseudotracheae, arranged nearly parallel to one another from the outer to the inner margin of the labella, where they, in part, join anteriorly a large pseudotracheal stem, extending toward the middle of the disk formed by the labellae, and, in part open directly into the triangular central opening between the labellae, their basal ends being supported by rods which radiate from a strongly chitinized ring around this opening. Between the bases of the rods supporting the inner ends of the pseudotracheae are teeth, which are concealed when the labellae are not opened very widely.

The structure and functions of the fulcrum, and the minute structure and mode of use of the pseudotracheae are left for further discussion later.

Leaving the part of this paper which is more exclusively devoted to the descriptions of the structure and arrangement of the mouth-parts and suctorial apparatus of the four diptera *Culex, Bombylius, Eristalis* and *Musca*, which I have studied, I turn to the portion of my paper devoted to the

COMPARISON OF THE MOUTH-PARTS AND SUCTORIAL APPARATUS IN DIFFERENT FAMILIES OF *DIPTERA.*

In this division of my paper, while I shall, for the most part, make use of results derived from my own examination of *Culex, Bombylius, Eristalis* and *Musca*, for these four genera make a fine series for most purposes of comparison, I shall not hesitate to take advantage of the results of the researches of others, so far as I think them trustworthy and suited to my purpose, but, in all cases, giving credit, as far as possible, to those from whom I obtain anatomical facts. I shall try, in this portion of the treatment of my subject, to present briefly, together with my own ideas, the views, theories, homologies and nomenclature, which have been adopted by various authors for the mouth-parts of diptera, so far as their views pertain to parts under my consideration.

The first organ which I shall examine comparatively in this paper is the fulcrum. In *Eristalis*, the fulcrum (side view, pl. 3, fig. 7; cross-section, fig. 1, ε', $d'fpf$) consists of a hollow frame of chitin, comparable to a somewhat irregular, much compressed, truncated cone, with a deep sinus in each of the flattened sides of its larger, or basal, end. This fulcrum is suspended, by the longer of the two processes (fig. 7, d') of its basal end, in the anterior angle (fig. 1, d) of the front of the head, — with its apex reaching nearly to the middle joint of the proboscis, — in such a way as to swing on the point d as an axis. In figs. 2 and 3 (of pl. 3) it would occupy the space filled by the pharynx (p) and the pharyngeal muscles (pm); pendulous around the point d, in the extension and retraction of the proboscis. The under, or ventral, portion of the inside of the fulcrum is occupied by the pharynx (fig. 1, ε', p); its upper, or dorsal, portion by the pharyngeal muscles (pm). In *Musca vomitoria* the fulcrum (in cross-section, pl. 4, fig. 4) is of similar general outline as in *Eristalis*, as can be seen in pl. 4, figs. 2 and 3, where it would occupy the space filled by the pharynx (p) and the pharyngeal muscles (pm); its posterior

margin, more sinuate than it is in *Eristalis*, is indicated by the dotted line *dz*. Its posterior ventral horns here project backward on each side of the oesophagus. In *Musca* the fulcrum is not as much compressed laterally as it is in *Eristalis*, as can be seen by comparing its sections in the two. (Compare pl. 3, fig. 1, ε', $d'fpf$, and pl. 4, fig. 4.) In both *Musca* and *Eristalis* the fulcrum contains the pharynx and pharyngeal muscles, but in *Musca* the latter are divided into two portions (pl. 4, fig. 4, *pm*). Another peculiarity of the fulcrum in *Musca*, a peculiarity not very evident in *Eristalis*, becomes very marked; that is, that its walls fail on the upper side of its anterior extremity, so that a cross-section of the fulcrum, as seen in pl. 4, fig. 1, β', fff, is nearly U-shaped, and the upper opening is closed over by the elastic membrane (*c*) which forms the outer walls of that portion of the proboscis. In *Eristalis* the upper wall is really absent from the anterior end of the fulcrum, altho its absence is not as marked as it is in *Musca*. In pl. 3, fig, 1, δ', the chitinous portions and the muscles directly around the pharynx (*p*) are parts of the extreme anterior end of the fulcrum and its contents, and are without upper covering-walls. The above-mentioned absence of the upper wall on the anterior end of the fulcrum of *Eristalis* and of *Musca* allows, when the proboscis is retracted, the labrum to sink its convexity into the flexible membrane, which bridges from one side of the fulcrum to the other, in the basal portion of the proboscis. Cross-sections of the fulcrum (pl. 3, fig. 1, ε', $pfd'p$, and pl. 4, fig. 4) show that its ventral part consists of two plates of chitin, the outer plate firmer than the inner, united above on each side, that is, the inner plate is sprung into the concavity of the outer one, so that, at rest, on account of the elasticity of the inner plate, but little space remains between the plates; this space is the pharynx. Upon the upper surface of the chitin plate which forms the upper wall of the pharynx are inserted the pharyngeal muscles, their origin being in the dorsal portion of the fulcrum. By their contraction the pharyngeal muscles enlarge the lumen of the pharynx, which is again diminished, upon their relaxation, by the elasticity of its upper wall.

The function of the fulcrum is, in the first place and most essentially, to furnish the frame-work of a suctorial organ, of which the motive power is the enclosed pharyngeal muscles, as dilators of the pharynx, opposed by the elasticity of the upper pharyngeal wall, as contractor of the pharynx. The function of suction was attributed by Réaumur[12] to the proboscis of *Musca;* he regarded the "trunk as a sort of suction-pump;" * but Gleichen[22] was the first to locate

* "... trompe comme une sorte de pompe aspirante." (p. 268.)

more definitely the pumping organ in the basal half of the proboscis, "which" he writes (p. 20), "may be indeed the real pump of the whole machine." * Lowne [23] (p. 41-42) gives an excellent description of how the parts of the fulcrum, which he calls the pharynx, act in pumping. A second function of the fulcrum in *Musca* and *Eristalis*, and one which will be seen later to be less constant throughout the diptera than the first function, is to support and control the motions of the basal half of the proboscis, of course controlling through its basal half many of the motions of the whole proboscis. On the posterior ventral processes of the fulcrum (pl. 4, fig. 2 and 3, *z*) are inserted muscles, which have their origins in the anterior, lateral part of the head; these muscles, by their contraction, project the base of the proboscis, by revolving the fulcrum about the point *d*, where it is attached.

The next question which naturally arises is, whether the fulcrum, more or less completely developed, is found, or not, in *Culex* and *Bombylius*. A hasty examination of the median longitudinal section through the head of *Bombylius* (pl. 2, fig. 3) shows that the portion comprised, in section, by the pharynx (*p*) and the pharyngeal muscles (*pm*) is an exact morphological counterpart of the section of the fulcrum in *Eristalis* and *Musca*. (Correspondingly lettered in pl. 3 and 4, figs. 2 and 3.) A cross-section of the fulcrum of *Bombylius*, near its distal end (pl. 2, fig. 1, λ', *ff*) shows that it consists, like the corresponding section in *Musca*, of the upper and under walls of the pharynx, extending upward and divergent, from each side of the pharynx, and having between its diverging walls the pharyngeal muscles (*pm*). The differences in structure between this fulcrum of *Bombylius* and that of *Musca* and *Eristalis* are such as are due to the fact that the proboscis of *Bombylius* is not extensible, and, consequently, that its fulcrum need not be movable about an axis at *d* (pl. 2, fig. 3). This absence of motion of the fulcrum around an axis allows the fulcrum to be less independently suspended in the head than it otherwise would be; its upper side consequently fails, its lateral chitinous walls are attached to the anterior wall of the head, and the pharyngeal muscles have their origin on the wall of the head. The distal extremity of the fulcrum of *Bombylius* serves, as it does in *Musca*, for attachment for the bases of the labrum-ephipharynx and hypopharynx. Here, then, in *Bombylius*, the fulcrum retains its essential anatomical characters, and its function as a suctorial organ; but is less independently movable than in *Musca* and in *Eristalis*, and its position is inside the head.

* "... Welches wol die eigentliche Pumpe der ganzen Machine seyn mag."

In *Culex* the part which corresponds to the fulcrum of *Musca* is a trifle less easily recognizable than it is in *Bombylius*. By an examination of the longitudinal median section of the head of *Culex* (pl. 1, fig. 11) it is easily discoverable that, just behind the place where the mouth-parts join to form the mouth, a set of pumping muscles exists similar to those found in *Musca* and *Eristalis*. These muscles are, however, enclosed in a chitinous case or box (fig. 11, *c*) of their own in front of the head. By studying cross-sections through this box (pl. 1, fig. 9, in female; fig. 15, in male), the muscles (*pm* and *pm'*), which have their origins in the upper and lateral portions of this chitinous case, are inserted on the basal supports of the labrum-epipharynx, in the same general way as they are attached to the pharyngeal walls in the fulcra already described; and that, by their contraction, these muscles would serve, in the same way as has been already described, to separate from each other the upper and lower walls of the pharynx. The upper and lower walls of the pharynx themselves have a similar form, in cross-section, to that which they have in *Musca* and *Eristalis*; their lateral portions turn upward and form a slight internal chitinous framework about the pharynx; on the upper walls of the pharynx originate the pharyngeal muscles. Here we have, then, as in all the diptera previously compared, a fulcrum, only that, in *Culex*, its upper portion is more rudimentary than is usual, the necessary rigidity for the origin of the pharyngeal muscles being supplied by the forward wall of the head (fig. 11, *c*). The position of the fulcrum in *Culex* is not essentially different, because located in a case apparently external to the head, from the position which it occupies in the basal part of the proboscis of *Musca*, when the proboscis is extended.

The relative position or condition of the fulcrum in the genera of diptera which I have most studied is this: in *Culex* it is permanently extended; in *Bombylius*, permanently retracted; and in *Eristalis* and *Musca*, capable of extension or retraction at will.

Before essaying to discover the homological significance of the fulcrum itself, it is well to turn attention to the parts which surround it. In *Bombylius* the chitinous wall (pl. 2, fig. 3, *c*) of the head, forming the covering to the upper, or dorsal, open side of the fulcrum, bearing, on its inner surface, the pharyngeal muscles, and continuous with the labrum in front, would, without doubt, be recognized as the clypeus (epistom of some authors). The chitinous wall which surrounds the fulcrum beneath, continuous at the sides with the clypeus above, is the under surface of the head. The under surface of the head is continuous anteriorly with the labium, but often, between the two, exhibiting folds, which (pl. 2, fig. 3, *l'*, *l''*) may be reckoned as belonging to the head or to the labium.

At the side one of these folds encloses the basal chitinous support of the maxillae as can be seen in pl. 2, fig. 1, x and λ', where the basal supports of the maxillae are lettered *x*, and the folds of the labium l' and l''. In *Culex* the same relative position and connection of parts are found, as can be seen in pl. 1, figs. 9 or 15, where the pharynx and its muscles are surrounded above by the clypeus (*c*), extending, at the sides, into the bases of the maxillae (*mx*) and of the maxillary palpi (*mp*), and continuing beneath into the walls of the basal portion of the labium. In *Eristalis* and *Musca*, when the basal half of the proboscis is retracted, the conditions are relatively the same as in *Bombylius*. (Compare pl. 3, fig. 2, and pl. 4, fig. 3, with pl. 2, fig. 3.) The clypeus (*c* on each pl.) extends downward, from the frontal angle (*d*) of the head, to the middle joint of the proboscis; at the sides, as can be seen in figures of numerous sections, the bases (*x*) of the maxillae, where maxillae exist, are in the base of the labrum (*l*) or in its fold (l'). The question, whether, or not, the portion represented in section in pl. 4, fig. 1, β', *x*, is the homolog of a basal portion of a maxilla is left for further consideration.

Having discussed the surroundings and functions of the fulcrum in *Culex*, *Bombylius*, *Eristalis* and *Musca*, the question remains, what is the fulcrum itself, homologically considered? Repeating, in some cases, what I have already said, in earlier parts of this paper, I will briefly state the opinions of several authors on this question. Gerstfeldt[3] figured the fulcrum of *Musca*, without assigning it a special name, and apparently without discovering that it was, strictly speaking, an internal organ. He considered the fulcrum to be made up of the maxillae, for the most part, united with the mandibles above and with the submentum of the under lip beneath. The incorrectness of Gerstfeldt's views of the construction of the fulcrum are evident when one sees, as already explained, that it is only the outer sheath around the fulcrum that is continuous with the under lip, and that the bases of the maxillae lay entirely independent and outside the walls of the fulcrum. The use of the name fulcrum, probably originated from the following remark of Lowne[23] (p. 42): "Although I believe this organ is homologous to the fulcrum in bees, I prefer the term pharynx, from its double connection with the mouth and oesophagus, as well as its peculiar function." Macloskie[24] says (p. 154): "One of Lowne's terms for it (pharynx) is incorrect; it is rather a case surrounding the pharynx. I shall refer to it by the name fulcrum." Macloskie later (p. 159-160) expresses the view that the "mid-segment" of the so-called proboscis, "is the true base of the fly's proboscis", and homologizes the fulcrum with the endocranium of the cockroach (*Blatta*); he also says of the fulcrum "It seems to be general in diptera; even the mosquito possesses it," but he does

not further describe it, in other diptera than *Musca*. Menzbier[8] writes (p. 64) of the fulcrum, without attempting further to homologize it, that, "it is chitinized processes of the walls of the throat." * It is probably the fact that the fulcrum is only a modified form of chitinization of the walls of the pharynx, which are turned upward at the sides, and fastened, more or less firmly, to the under side of the clypeus; in cases where independent motion of the entire pharynx takes place in the extension and retraction of the proboscis, the lateral upward continuations of the pharyngeal walls may unite again above, to a greater or less extent, so as to form a cylinder for the firm attachment above of the pharyngeal muscles, which thus act with equal ease to whatever extent the proboscis may be withdrawn or stretched out. The whole plan of structure of an independently movable fulcrum is well shown in the section of the fulcrum of *Musca* figured on pl. 4, fig. 4. The fulcrum is, then, an internal skeletal piece, the chitinized expanded portion of the walls of the pharynx, and not a mouth-part in the strict sense of the term. The reason will now be more apparent, why, in an earlier part of this paper (p. 26), I objected to laying too much stress on the division of the proboscis into basal, middle, and terminal portions. While applying the term proboscis, in its ordinary sense, to the whole organ, I agree with Macloskie that the so-called middle portion of the proboscis is the true basal segment of the fly's proboscis. I may, perhaps, add, at this point, that my reasons for using the somewhat clumsy term labrum-epipharynx, in place of the name operculum, applied by Lowne to the same part in *Musca*, are that, first, the name operculum is inappropiate in some diptera, and that, secondly, the name labrum-epipharynx saves all confusion of parts by indicating, at first sight, what mouth-parts are meant.

If one considers, in order, the different mouth-parts of diptera, they are as follows:

The labrum-epipharynx is composed of the labrum above and the epipharynx beneath, united at their margins by a delicate membrane, which is often infolded (*Bombylius*). The labrum and epipharynx may be separable in caustic potash (*Musca*) or inseparable (*Empis* according to Menzbier). The epipharynx may be absent, according to Menzbier (*Sargus*). At its base the labrum-epipharynx may be united to the apical end of the fulcrum by a true joint (*Musca*), or without joint (*Culex*); the labrum is always continuous with the clypeus at the base, the epipharynx always continuous with the upper wall of the pharynx. The labrum-

* " . . . es chitinizirte Fortsätze der Schlundwand sind.

epipharynx may have a single point at its tip (*Musca, Bombylius*) or may end, apically, in several points (*Culex,* and probably all *Syrphidae*). The labrum-epipharynx usually forms a cover for the channel of the labium below, and may be separable from the labium, at the will of the insect (*Culex*), or may remain always tightly closed over the labium (*Musca*). The labrum-epipharynx is usually, second to the labium, the largest mouth-part of a dipteron. Within it may contain muscles and tracheal stems (*Bombylius* and *Musca*). The channel of the epipharynx is never completely cylindrical, but is slightly open along its under side; a tube is formed by the pressing of the hypopharynx upward against this opening; through the tube thus formed the food is sucked up to the mouth.

The hypopharynx is usually present in diptera (according to Menzbier absent in *Sargus*), and contains a tube, opening by a channel on its upper surface; this channel extends back, more or less, from the tip, and is the outlet for the salivary secretion. The tip of the hypopharynx may be naked and used as a lance (*Haematopota*, according to Menzbier), or may be hairy (*Musca*). The upper side of the base of the hypopharynx is continuous with the lower wall of the pharynx; its under surface may entirely coalesce with the labium (*Culex*, male), may join the labium more or less anterior to the mouth (*Musca*), or, if either mandibles or maxillae are present, its base may join them (*Culex,* female).

The mandibles are the mouth-parts which are least developed, or most often absent, in diptera. They are present in *Culex,* female, and, according to Menzbier, in *Haematopota*; they are absent in *Eristalis, Bombylius, Musca,* and many other diptera. When present they are usually delicately lamelliform.

The maxillae are, next to the mandibles, the oftenest absent in diptera; but when both maxillae and mandibles are present (*Culex,* female), the maxillae are more developed than are the mandibles. Maxillary palpi are usually, probably always, present in diptera, usually joining the maxillae at the base; they are from one-jointed (*Bombylius, Eristalis, Musca*) to five-jointed (species of *Culex*), are more or less hairy, and lay outside the proboscis, attached near or at the mouth. The position of the maxillary palpi in *Musca* has evidently created much confusion in the homology of the parts of the proboscis of these insects. Their location on the membranous bridge between the two upper edges of the distal end of the fulcrum (in section, pl. 4, fig. 1, β', *mp*) seems to have led Gerstfeldt [3] to regard the fulcrum itself as chiefly made up of the maxillae. Gerstfeldt described two processes extending back from the base of his hypopharynx (really the epipharynx), and figured them as inside the fulcrum. These processes he regarded as the basal portions, or "cardines," of the hypopharynx; a view which

is necessarily incorrect because his hypopharynx was the real epipharynx separated by caustic potash from the labrum. Lowne[23] (p. 43) mentions and figures these processes which he terms "apodémes," and, as he incorrectly supposed the labrum-epipharynx, his operculum, to be made up of the labrum with a maxilla coalesced on each side, he regards these "apodémes" to be the basal portions of the maxillae. Thus from incorrect premises Lowne arrived at what I consider to be a correct conclusion, that is, that these processes are the basal portions of undeveloped maxillae. Macloskie[24] regarded these same chitinous rods as the "great tendons" of the mandibles, and then added (p. 159) the impossible idea, "This will make the operculum represent two united mandibles, probably enclosing the labrum." Macloskie correctly says, however, of these "great tendons," that they are to the right and left of the fulcrum, and that they are slightly articulated to the operculum. Menzbier[8] writes (p. 65) of these same parts, in a very indeterminate manner, that, "they are simple muscle-tendons, which were less developed in *Syrphus*, and consequently not described by us." * That these processes really are the remnants of the basal chitinous supports of the maxillae is very probable, because they are the only chitin-rods which occupy the relative position that is occupied by the corresponding parts in other diptera (compare pl. 4, fig. 1, β', x with pl. 1, figs. 9 and 15, mx and mp; pl. 2, fig. 1, ι-λ', x; and pl. 3, fig. 1, γ'-ε', x); because they are imbedded in a fold of the base of the labium; because they are not firmly joined to the labrum, or to any other mouth-part; and lastly, because the maxillary palpi, altho not joined to these processes, are above their distal ends, a position they would scarcely reach if these chitinous tendons belonged to the mandibles or labrum. The maxillary palpi of *Musca* are not joined to any firm supporting piece; the bridge or band of chitin, seen at their base in pl. 4, fig. 1, is only a slight corrugation (as can be seen by the section represented in pl. 4, fig. 1, β', c), which is probably due to the hinderance to irregular folding, — which would be otherwise caused at that point when the proboscis retracts, — by the presence of the palpi themselves. The maxillary palpi of *Musca*, then, by some cause, are displaced from their basal supports, which remain in their places, without maxillae or palpi, performing, by the muscles attached to them, another function, that is, the lateral swinging of the proboscis when the insect is feeding.

The labium of diptera, their most fully developed mouth-part, and one that is always present, joins the head below the other mouth-parts; its under wall

* "Es sind einfach Muskelsehnen, die bei Syrphus weniger entwickelt und deshalb von uns nicht beschrieben sind."

is continuous basally, sometimes with folding, into the under wall of the head. The labium is usually somewhat fleshy, containing muscles and two longitudinal tracheal stems, and is hollowed out along the upper side to form a trough for containing other mouth-parts. At each side of the tip, the labium, probably in all cases, has more or less developed labellae, on the inner surface of which are usually the channels termed pseudotracheae. These pseudotracheae may be absent, however, as in *Culex*. The labellae are fleshy in *Musca*, less so in *Eristalis*, and least so in *Bombylius* and *Culex*. While the labium of all insects is undoubtedly the product of a coalesced pair of appendages, as Savigny supposed, and its parts can be still further safely homologized, in many insects, with particular portions of the maxillae, and altho it has been divided in Orthoptera and some other insects into submentum, mentum, glossa, etc., I do not believe that in the diptera, our knowledge of the structure of the labium suffices for us to enter safely on homologies of its parts, and I have, consequently, refrained from doing so in the preceeding pages.

The mode of separation and approximation of the labellae is somewhat different in different diptera, and is, perhaps, worthy of a comparative notice in this place. As already mentioned (p. 18), the labellae of *Culex* are attached to the tip of the labium by a true joint, and have, each, a flexor and extensor muscle. The labellae of *Bombylius*, described briefly on p. 25, altho not connected to the labium by a true joint, have each a flexor and extensor muscle. When, however, one examines, by sections, the labellae of *Eristalis*, which I have briefly described on p. 30, one finds only an extensor muscle in each labella, and in the sections of the labellae of *Musca* one finds no muscles. How, then, is the separation of the labellae effected in *Musca*, for both in *Musca* and in *Eristalis* their normal condition seems to be that of opposition? Examining the sections of the labellae of *Eristalis* (pl. 3, fig. 1, α') one sees that a chitinous band passes through the middle of each labella, and that, to the outer side of this band, the extensor muscle is attached. The bands serve as supports for the labellae, and as attachments for their extensor muscles; and these bands are themselves jointed at their bases to the inner or upper chitinous wall of the labium. An examination of cross-sections of the labellae of *Musca* shows this same chitinous band, but no muscle. The reason for the absence of the muscle is that, as has been already described (p. 36), the muscle does not extend into the cavity of each labella, but is only inserted on the base of these chitinous bands. The labellae of both *Musca* and *Eristalis* are opened, then, at least in part, by muscular force; but probably the more complete separation of the two labellae is caused by the same inflation with air, which, as previous writers have supposed,

serves to protrude, and to press firmly, the inner surfaces of the labellae, upon any surface from which the insect wishes to scratch or dissolve substances for food. That it is air, at least for the most part, and not water, which expands the inner surfaces of the labellae, is easily proved by pressing carefully the head of a fly between the fingers until the proboscis is fully extended, and the labellae fully inflated, then, putting the fly under water, and pricking with a needle the inner surfaces of the labellae; they will at once collapse, bubbles of air escaping, at the same moment, from the opening made in their surfaces by the needle.

The pseudotracheae on the inner surfaces of the labellae of *Musca* are cylindrical channels, sunk, more or less deeply, into the surface of the labellae, according to the amount that that surface is inflated, and they open on the surface in zigzag slits. These channels are held open by partial rings, more strongly chitinized than the rest of the membrane of the cylinder. As seen from above in *Musca domestica*, the pseudotracheae (pl. 4, fig. 6, *b*) appear to be supported by partial rings, one end of each of which is forked. Such a ring, if isolated, would appear as in fig. 6, *d*. These rings are apparently arranged so that one has its fork on one side of the opening of the channel, the next ring the fork on the opposite side of the channel, and so on, in alternation. This, I say, is the apparent structure, for if one expands the membrane of the inner surface of the labellae, to a sufficient extent, the channels, or pseudotracheae, are flattened out and their true structure is revealed. Pl. 4, fig. 7, represents a portion of such a flattened out pseudotrachea of *Musca domestica*, the structure of which is immediately evident; at the right-hand side of the figure is represented an irregularity, such as now and then occurs in pseudotracheae. If such a piece of flattened pseudotracheae as is seen at the left, in fig. 7, be formed into a cylindrical channel, its appearance will be as in pl. 4, fig. 6, *b*. In *Musca vomitoria* the pseudotracheae have a structure somewhat different in detail, but not in principle, from those already described, as can be seen from fig. 5 without further description. The pseudotracheae of *Eristalis horticola* are so nearly like those of *Musca vomitoria*, that I have not figured those of the former. Pl. 4, fig. 8 represents a section through a portion of the inner surface of a labella of *Musca vomitoria*, cut at right angles to the direction of the pseudotracheae which pass through it; in this section the intrapseudotracheal spaces are represented as protruded beyond the edges of the pseudotracheae themselves; this is the natural position of the pseudotracheae in repose, but when the fly inflates his labellae in the process of eating, the soft intrapseudotracheal membrane is stretched, and the margins of the pseudotracheae are protruded beyond the general level of the surface of the

labella. These margins of the pseudotracheae consist of the lobes, or teeth, to be seen at each side in pl. 4, fig. 7. The ring-like structure of pseudotracheae has the same function as the similar structure in the tracheae of insects, or in the wind-pipe of vertebrates, that is the function of holding tubes open, and preventing their sides falling in upon one another. The same peculiar ring-like structure is also found, with like functions, in the salivary ducts of diptera. If the labellae are now alternately inflated, a little more and then a little less, the width of the zigzag openings of the pseudotracheae is alternately increased and diminished, and the teeth along the margins of the cleft naturally scratch on the surface on which the fly has pressed his labellae. The same scratching effect is produced when the labellae are simply moved a little back and forth upon any surface. The labellae are, then, files of which the teeth are the serrate edges of the pseudotracheae. During the scratching process the pseudotracheae are, in *Musca*, moistened with saliva, with which they wash the surfaces of the substance to be scratched or dissolved away. Lowne[28] says of the pseudotracheae (p. 47-48) "these form a fine strainer through which the insect is enabled to filter the fluid from the solid portion of the substances on which it feeds." In *Bombylius* — which offers excellent facilities for studying the pseudotracheae, because they, altho constructed on the same principles as, are more firm and consistent than, in *Musca*, — I have found that, after feeding the fly with a mixture of sugar and gum-arabic, colored with carmine, and then plunging it suddenly into strong alcohol to fix the colored solution in its mouth-parts, that, later, when I cut sections of its labellae, the pseudotracheal teeth, instead of having their ordinary position (see pl. 2, fig. 5, *a*; in section, fig. 6. *a*), were turned outward from the pseudotracheal channel, into the position seen in pl. 2, figs. 5 and 6, *b*, and that the colored solution of gum-arabic had not entered the pseudotracheae. *Bombylius* also rubs the labellae over the surface of the substance on which it is feeding, in a way similar to that which *Musca* does. It can be seen that the more purely liquid food any species of diptera eat, for a constant diet, the less necessary and the less developed are the pseudotracheae; *Culex*, for example, eating a purely liquid food, has no pseudotracheae. From the above facts, I am led to think that the primary function, at least, of the pseudotracheae of diptera is to file away substances on which they feed. That the pseudotracheae may have other functions, I do not wish to affirm or deny.

The pharyngeal sucking organs of the four different genera of diptera which I have studied have been so fully compared in the comparison of the fulcra in

these genera, that I need not further refer to them. The oesophageal bulb, as sucking apparatus, behind the oesophageal nerve-ring, exists, as far as I know, only in *Culex*, and cannot therefore be compared with any other like structure; and I will here end my notes on the comparative structure of the mouth-parts and suctorial apparatus of the diptera, whose examination and dissection furnished me the materials for this paper.

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VITA.

The only child of George Monroe, and Elizabeth Learned Dimmock, I, George Dimmock, was born the 17th of May 1852, in Springfield, Massachusetts, U. S. A.

After several years of study in the public schools of my native city, I was fitted, at the Harvard School, a private school in Springfield, to enter Harvard College, Cambridge, Massachusetts, which I entered in 1873, and from which, on graduation in 1877, I received the degree of bachelor of arts, with honors in natural history.

In October 1879, I was matriculated, as student of natural history, in the University of Leipzig, where I remained until the autumn of 1881. In Leipzig my time was chiefly devoted to the study of zoology in the laboratory of Professor Leuckart, in addition to whose lectures, I attended lectures by Professors Carstanjen, Carus, Credner, Schenk and Wiedemann, and by Doctors Chun, Fraisse, von Ihering, Luerssen and Marshall.

EXPLANATIONS OF THE PLATES.

The following letters have the same signification on all the plates:

c, clypeus; *c'*, its folds.
e, epipharynx.
f, fulcrum.
h, hypopharynx.
i, infraoesophageal ganglion.
l, labium; *l'*, *l''*, its folds.
lb, labellae.
lr, labrum.
lr-e, labrum-epipharynx.
m, mandibles.
mp, maxillary palpi.
mx, maxillae.
oe, oesophagus.
p, pharynx.
pm, *pm'*, pharyngeal muscles.
s, supraoesophageal ganglion.
tr, tracheal stem.
x, basal support of maxillae.

The number of diameters enlargement is indicated against each figure.

Greek letters are used to indicate where sections are made in probosces, and the corresponding sections are indicated by the same letters, often with an accent (').

Shaded parts of sections are portions filled with connective tissue, nerves, air-spaces, and other parts having no significance in connection with points discussed in the dissertation.

EXPLANATIONS OF PLATE I.

Fig. 1.—Side view of head of *Culex rufus*, with extended mouth-parts; *a*, antennae.

Fig. 2.—Same from above with mouth-parts partly cut away.

Fig. 3.—Tip of labium of female *Culex*.

Fig. 4.—Tip of labium of male *Culex*.

Fig. 5.—Tips of separated setae of mouth-parts of *Culex*.

Fig. 6.—Tip of labrum-epipharynx seen from beneath and in section.

Fig. 7.—Cross-section through the labellae and tip of labium of female *Culex*.

Fig. 8.—Cross-section near the middle of the proboscis of female *Culex*.

Fig. 9.—Cross-section through pharyngeal region of the forward part of the head of female *Culex*.

Fig. 10.—Cross-section through the posterior part of the head of female *Culex*, to show the sucking bulb of the oesophagus. *b*, lumen of the oesophageal bulb. *bm* and *bm'*, muscles to dilate the bulb. *r*, chitinous rods which support the oesophageal bulb. *rm*, retractor muscles of the maxillae, at their point of origin. *t*, elastic plates of sides of bulb.

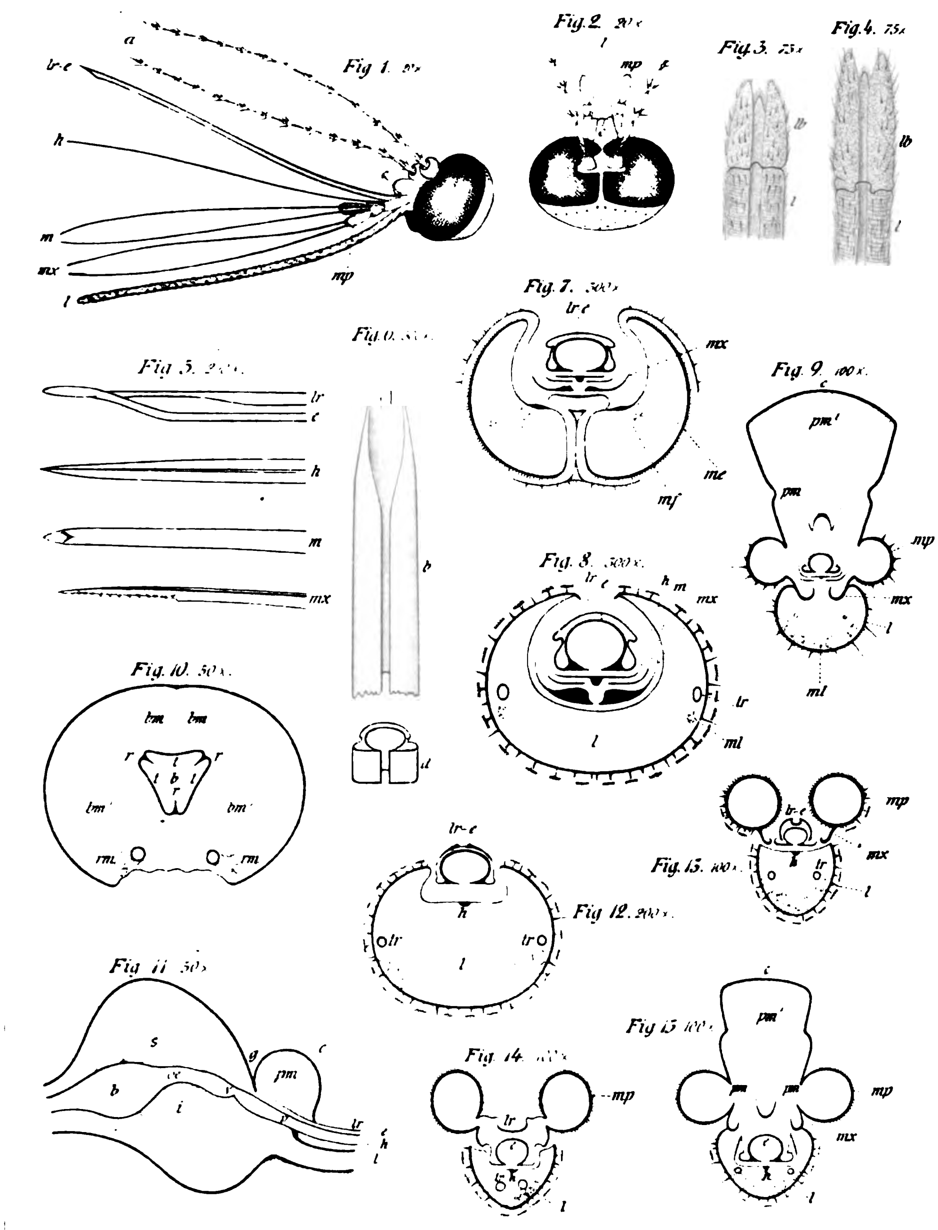
Fig. 11.—Longitudinal section of the head of a female. *Culex*. *b*, oesophageal bulb. *g*, point where the clypeus appears cut off from the rest of the head. *v*, valve between pharynx and oesophagus.

Fig. 12.—Cross-section near the middle of the proboscis of a male *Culex*.

Fig. 13.—Cross-section at the base of the proboscis of a male *Culex*.

Fig. 14.—Cross-section further into the base of the proboscis of a male *Culex*.

Fig. 15.—Cross-section through the pharyngeal region of the head of a male *Culex*.



EXPLANATIONS OF PLATE II.

Fig. 1.—Side view of the head of *Bombylius major* with its proboscis; at the upper right-hand corner are figured the tips of the labrum-epipharynx, hypopharynx and maxilla, to illustrate their comparative sizes and lengths. Below (α—λ') is a series of cross-sections of various parts of the proboscis and its base.

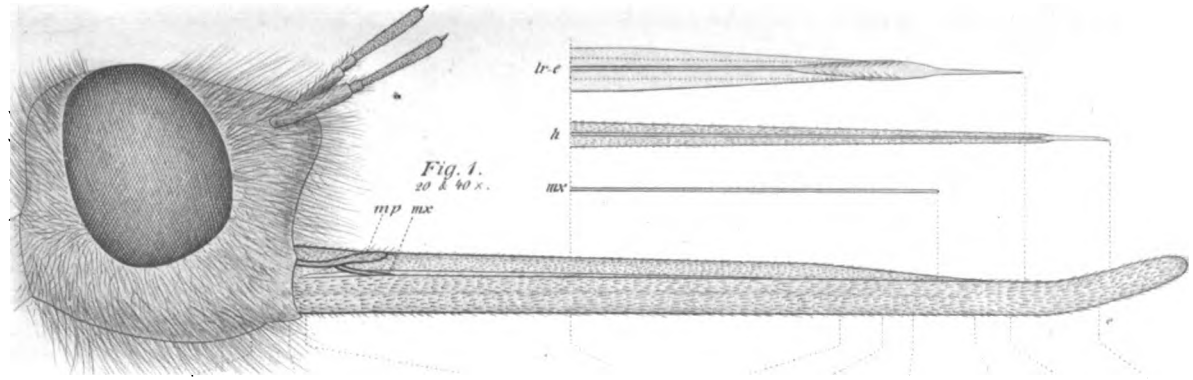
Fig. 2.—View of the head of *B. major* from above, to show how the labellae open.

Fig. 3.—Longitudinal section of the head of *B. major*. *z*, location where the ventral posterior process of the fulcrum lays. *d*, location of the dorsal posterior process of the fulcrum.

Fig. 4.—Tip of maxilla of *B. major*.

Fig. 5.—Perspective view of the chitinous portions of the pseudotracheae of *B. major*; *a*, while at rest; *b*, while feeding.

Fig. 6.—Cross-sections of the pseudotracheae of *B. major* when the two labellae are opposed to each other; *a*, at rest; *b*, while feeding.



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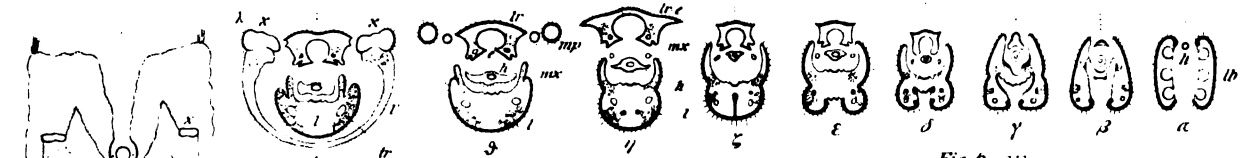
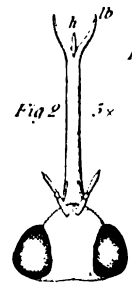


Fig. 6. 200 ×



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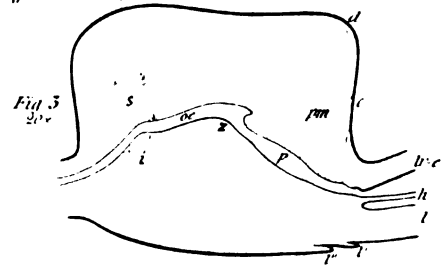

Fig 3
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Fig. 4. 400 ×.

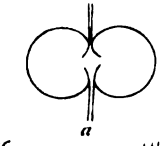

Fig. 5.
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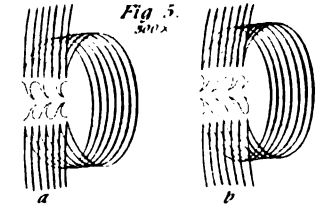

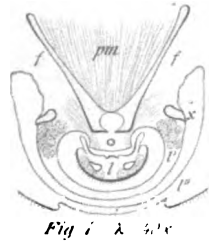

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EXPLANATIONS OF PLATE III.

Fig. 1.—Side view of the head of *Eristalis horticola*; dotted lines indicate the courses of the tip of the proboscis, *k*, and of its middle joint, *g*, in the retraction of the proboscis. *d*, angle of the head in which the dorsal posterior process, *d'* (fig. 7), of the fulcrum is attached.

Fig. 2.—Longitudinal section of the head of *E. horticola*, with partly retracted proboscis. Lettering as in fig. 1.

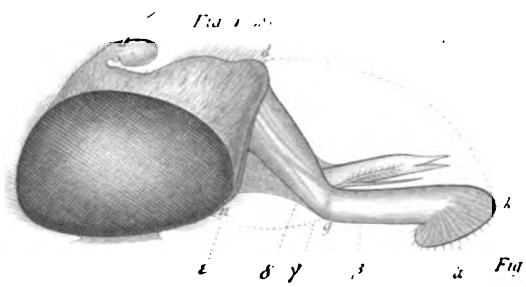
Fig. 3.—Longitudinal section of the head of *E. horticola*, with extended proboscis. Lettering as in fig. 1 and 2.

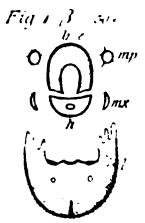
Fig. 4.—Detached maxilla and maxillary palpus of *E. horticola*.

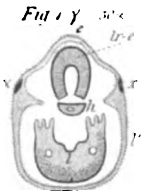
Fig. 5.—Tip of labrum-epipharynx of *E. horticola*, spread out and viewed from beneath.

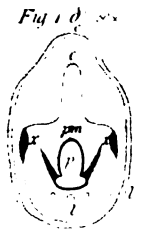
Fig. 6.—The hypopharynx of *E. horticola*, from above.

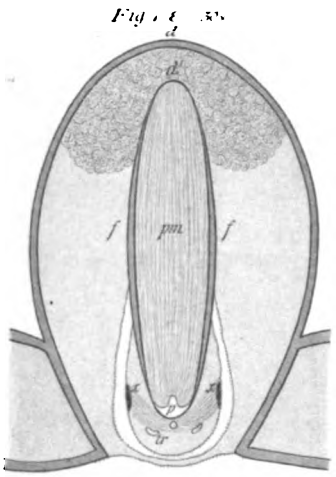
Fig. 7.—The fulcrum of *E. horticola*; *d'*, its dorsal posterior process; *z*, its ventral posterior process.

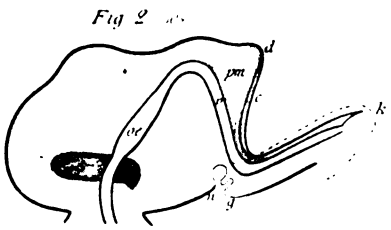


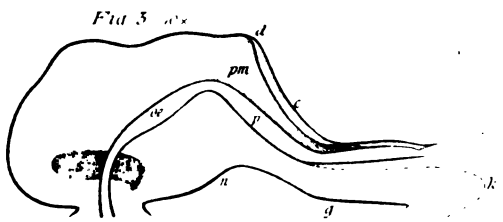


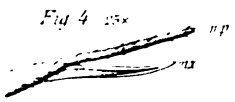


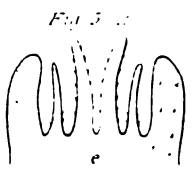


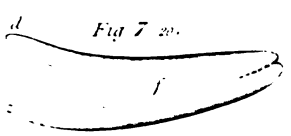












EXPLANATIONS OF PLATE IV.

Fig. 1.—Side view of the head of *Musca vomitoria*, with extended proboscis.

Fig. 2.—Longitudinal section of head of *M. vomitoria*, with extended proboscis. *sd*, salivary duct. *d*, dorsal posterior process of the fulcrum. *v*, ventral posterior process of the fulcrum. [In this and the next figure the section of the frontal sac is omitted to avoid complicating the figures.]

Fig. 3.—Longitudinal section of the head of *M. vomitoria*, with partly retracted proboscis. Lettering as in fig. 2.

Fig. 4.—Section of the fulcrum of *M. vomitoria*.

Fig. 5.—Pseudotrachea of *M. vomitoria*.

Fig. 6.- Pseudotrachea of *M. domestica*; *d*, one of the apparent segments of the pseudotrachea.

Fig. 7.—A portion of a pseudotrachea of *M. domestica* spread out to show its real structure; toward the right it is abnormal.

Fig. 8.—Cross-section of three pseudotracheae of *M. domestica* to illustrate their position in the surface of the labella.

Fig 1

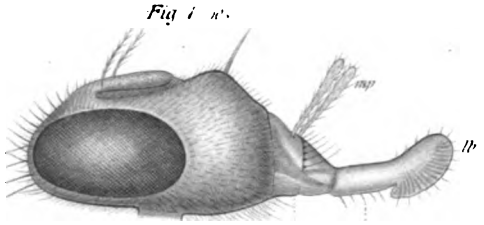


Fig 1 α'

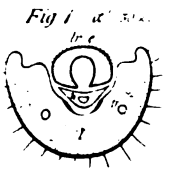


Fig 1 β'

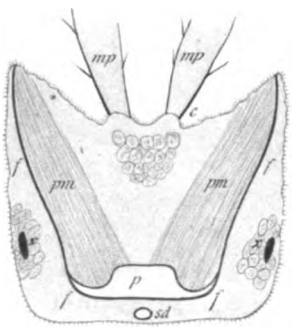


Fig 2

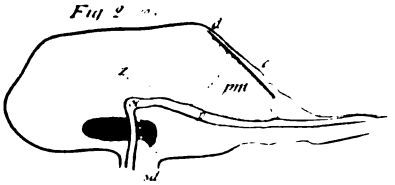


Fig 3

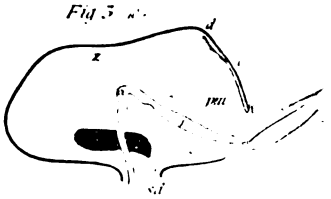


Fig 4

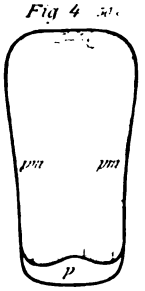


Fig 5

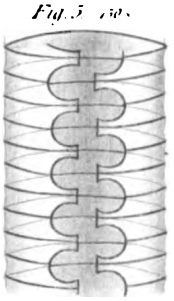


Fig 6

Fig 7

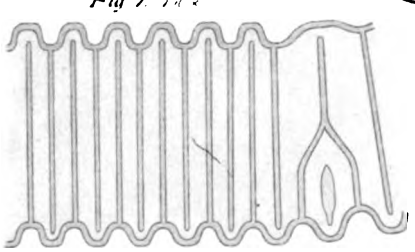
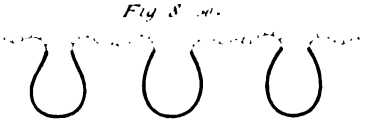


Fig 8



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